

Recent Advances in Science in Western Australia

Earth Sciences

The main aquifers of the upper Murchison River catchment are described in a review by A T Laws of the Geological Survey of WA as calcrete and alluvial deposits in drainage lines with generally <15 m water depth. Other supplies are from weathered bedrock, sedimentary rocks and fractured rocks in the greenstone belts. Water salinity is low beneath drainage divides, and increases towards and down drainage lines.

Laws A T 1992 Hydrogeology of the upper Murchison River catchment. Western Australian Geological Survey Record 1992/6.

M E Barley of the University of Western Australia reviews Archean volcanic-hosted sulfide mineralization in Western Australia. The deposits which range in age from about 3.5 to 2.7 Ga occur mainly in areas of greenschist facies metamorphism in the Warrawoona, Gorge and Whim Creek Groups (eastern and western Pilbara Cratons), and the Norseman-Wiluna and Golden Grove belts (Yilgarn Craton).

Barley M E 1992 A review of Archean volcanic-hosted massive sulfide and sulfate mineralization in Western Australia. Economic Geology 87:855-872.

The Darling Range bauxite deposits, which supply about 17% of the world's alumina, are described in detail by R Anand (CSIRO), R Gilkes (University of Western Australia) and R Cotton (Alcoa). Gibbsite is the dominant form of Al in these deposits, which differ in chemical and mineralogical properties from other Australian deposits.

Anand R R, Gilkes R J, & Roach G I D 1991 Geochemical and mineralogical characteristics of bauxites, Darling Range, Western Australia. Applied Geochemistry 6:233-248.

A major nickel resource, that was originally discovered in 1971, has been delineated within a lensoid sulphide body at Digger rocks, in komatiitic volcanic in the Forrestania greenstone belt of the Yilgarn Craton.

Woodhouse M, Cox R, & Cotton R E 1992 Economic geology of the Digger Rocks nickel deposit, Forrestania, Western Australia. AusIMM Proceedings 297:31-43.

Descriptions by P E O'Brien of the BMR (Canberra) and N Christie-Blick of the Doherty Geological Observatory (New York) of grooved surfaces in the Carboniferous/Permian Grant Group confirm that there were large continental ice sheets during the Late Palaeozoic glaciation. Pebbles of banded iron-formation in marine diamictites associated with the grooved surfaces indicate motion of ice from 400 km to the south in the Pilbara Craton.

O'Brien P E & Christie-Blick N 1992 Glacially grooved surfaces in the Grant group, Grant Range, Canning Basin and the extent of Late Palaeozoic Pilbara ice sheets. BMR Journal of Australian Geology and Geophysics 13:87-92.

A regional study of deep formation waters by researchers from the BMR (Canberra) and ANU contributes to an assessment of groundwater resources and genesis of Mississippi Valley style Pb-Zn deposits. There is a wide salinity range from almost fresh water to brine water, most of which is in the Willara and Kidson Sub-basins that were sites of sabkhas and extensive evaporite deposits.

Ferguson J, Etiman H, & Ghassemi F 1992 Salinity of deep formation water in the Canning Basin, Western Australia. BMR Journal of Australian Geology and Geophysics 13:93-105.

Life Sciences

CSIRO entomologists J K Scott and E S Delfosse census 251 South African plants introduced to Australia, of which 68 are weeds of importance to agriculture, forestry and conservation. This review ranks the weeds in importance of biological control, prioritizes future research, and provides an extensive bibliography.

Scott J K & Delfosse E S 1992 Southern African plants naturalized in Australia: a review of weed status and biological control potential. Plant Protection Quarterly 7:70-79.

K Christian of the Northern Territory University and S Morton of CSIRO (Alice Springs) describe an exceedingly thermophilic central Australian ant which tolerates body temperatures up to 56.7°C. The ants are active during the hottest periods of summer, preferring to be active at surface temperatures about 60°C and avoiding temperatures less than 56°C.

Christian K A & Morton S A 1992 Extreme thermophilia in a central Australian ant, *Melophorus bagoti*. Physiological Zoology 65:885-905.

A study of the goanna *Varanus gouldii* at the Karrakatta Cemetery, Perth, by G Thompson of the University of Western Australia and Edith Cowan University, indicates that daily movements of lizards were erratic and variable. The average travel distance was about 110 m per day, and the daily foraging area was about 300 m².

Thompson G 1992 Daily distance travelled and foraging areas of *Varanus gouldii* (Reptilia: Varanidae) in an urban environment. Wildlife Research 19:743-753.

The golden bandicoot, studied on Barrow Island by P Withers of the University of Western Australia, is a small, arid-adapted marsupial with a low and labile body temperature. In metabolic, hygric and thermal physiology, the golden bandicoot resembles the bilby and differs from temperate and tropical bandicoots.

Withers P C 1992 Metabolism, water balance and temperature regulation in the golden bandicoot (*Isodon auratus*). Australian Journal of Zoology 40:523-531.

In the latest edition of his book, H Cogger provides taxonomic keys and a detailed description and a colour plate for species of Australian amphibians and reptiles.

Cogger, H G 1992 Reptiles and Amphibians of Australia. Reed, Frenchs Forest, NSW.

The specific identity of the common goanna, *Varanus gouldii*, is brought into question by W Böhme of the Zoological Institute and Museum of Koenig (Bonn). He suggests that the species name *gouldii* should be applied to what is currently recognised as *Varanus panoptes*, and the currently recognised *V. gouldii* should be named *V. flavivirufus*.

Böhme W 1991 The identity of *Varanus gouldii* (Gray, 1838), and the nomenclature of the *V. gouldii*-species complex. Mertensiella 2:38-41.

S Garnett of the Royal Australasian Ornithologists Union considers the conservation status of all species or subspecies of Australia's threatened or extinct birds (14% of the total of 1074 bird taxa). He provides a summary of the status, distribution, habitat, remarks and references for each of the bird species or subspecies.

Garnett S 1992 Threatened and extinct birds of Australia. RAOU Report Number 82. RAOU, Moonee Ponds, Victoria.

D Pearson of the Department of Conservation and Land Management in his review of the past and present distribution of the black-footed rock-wallaby in the Warburton region of Western Australia, notes that the species was in a major decline by the mid 1970's and that continuing local extinctions require intervention for their long-term conservation.

Pearson D J 1992 Past and present distribution and abundance of the black-footed rock-wallaby in the Warburton region of Western Australia. *Wildlife Research* 19:605-622.

Macro-invertebrates, zooplankton and water quality parameters were used by researchers at Murdoch University and the Water Authority of Western Australia to classify and ordinate wetlands, and correlate the findings with environmental variables. The most nutrient enriched wetlands were dominated by cosmopolitan species with high abundances, whereas other wetlands had species with more restricted ranges and lower abundances.

Growns J E, Davis J A, Cheal F, Schmidt L G, Roswich R S & Bradley S J 1992 Multivariate pattern analysis of wetland invertebrate communities and environmental variables in Western Australia. *Australian Journal of Ecology* 17:275-288.

The phylogenetic relationships of Australian chelid turtles, investigated by A Georges (University of Canberra) and M Adams (South Australian Museum) using allozyme electrophoresis, revealed five distinct clades recognised at the generic level, *Elseya*, *Emydura*, *Rheodytes*, the *Elseya latisternum* group, and an undescribed species.

Georges A & Adams M 1992 A phylogeny for Australian chelid turtles based on allozyme electrophoresis. *Australian Journal of Zoology* 40:453-476.

The electronic data base of the Queensland Museum's register has been used by G Ingram and R Raven to map distributions of frogs, reptiles, birds and mammals of Queensland, prepare checklists of those species, and summarise the rare, endangered, vulnerable and poorly known species.

Ingram G J & Raven R J 1991 An atlas of Queensland's frogs, reptiles, birds and mammals. Queensland Museum, Brisbane.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA). Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. They are usually papers in referred journals, or books, chapters and reviews. Abstracts from conference proceedings will not be accepted. Please submit short (2-3 sentence) summaries of recent papers, together with a copy of the title, abstract and authors' names and addresses, to the Hon Editor or a member of the Publications Committee: Dr S D Hopper (Life Sciences), and Dr A E Cockbain (Earth Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters and suggest potential reviewers or respondents to your letter. P C Withers, Hon Editor, *Journal of the Royal Society of WA*.

Inside Evolution: 1992 Presidential Address

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Abstract

The relationship between an organism's life history, its ontogeny, and its evolutionary history fascinated biologists during much of the nineteenth century. However, with the shift in emphasis away from embryology to natural selection in the latter part of the century, the study of this relationship between ontogeny and phylogeny drifted into the backwaters of evolutionary theory. The last 15 years has seen a resurgence of interest in this topic. Recent studies have revealed that this relationship, known as heterochrony, plays a pivotal role in evolution, forming the link between genetics and natural selection. Heterochrony can be invoked to explain much intraspecific phenotypic variation, including polymorphism and sexual dimorphism. Many interspecific examples of heterochrony demonstrate that dissociation is a common phenomenon, with some features being paedomorphic (ancestral juvenile characters present in the adult), while others are peramorphic (ancestral adult characters present in the juvenile). Selection of heterochronic morphotypes is shown to focus sometimes on factors other than morphology. For instance, size or life history strategy might also be targeted. Extrinsic factors, such as predation pressure, are considered to play an important role in directing evolutionary trends that have been facilitated by heterochrony.

Introduction

A golden thread runs through the history of life. It is a thread that links sea urchins to apple maggot flies, snails to lungfishes, delphiniums to emus, and salamanders to humans. This connecting thread is the sequence of changes that occur to individual as it develops from embryonic to adult form. The importance of such changes was recognised by the ancient Greeks. Aristotle, for instance, believed that a sequence of increasingly more "complex" souls—nutritive, sensitive, then rational—entered the human embryo during its growth and development. What Aristotle and his contemporaries were recognising was the enormous and profound morphological changes that the human embryo, like the embryos of most other organisms, undergoes during early growth.

During the early part of the nineteenth century embryological studies dominated biological thought (Gould 1977). The great embryologist Karl Ernst von Baer recognised that similarities between animal's early developmental stages indicated an evolutionary relationship between such forms. While von Baer argued that it was invalid to compare directly the adult form of one animal with the juvenile stage of another, the realisation by some early 19th century palaeontologists that some sequences of fossils appeared to be arranged in a sequence comparable with embryonic changes led to the formulation of one of the great biological "laws" of the 19th century: the Law of Recapitulation.

Palaeontologists such as Louis Agassiz, who worked on fossil fishes in Switzerland in the 1830s and 1840s, argued, for example, that the form of the tail in adult fishes observed in the fossil record paralleled the development of the tail in modern fishes, from early embryonic stages to the adult stage. Thus the developmental stages of living teleosts often show that small juveniles have a simple tail, later juveniles a so called heterocercal tail, and final

juvenile a homocercal tail where top and bottom fins are the same size. This parallels the perceived evolutionary sequence (see McKinney & McNamara 1991, Fig 1-1).

But the one scientist to really promote this concept was Ernst Haeckel in the 1860's. In his most influential tome *Generelle Morphologie der Organismen*, Haeckel proposed his famous "Biogenetic Law" that was to become known to many future generations of biology students as "ontogeny recapitulates phylogeny"; an organism's developmental history, from fertilization to adulthood, contained within it the whole history of the evolution of that particular group. The argument was that our early embryos pass through stages that resemble, at one time worms, at another fishes, at another reptiles, before passing into a "mammalian" stage. The influence of Haeckel's work was profound. Many later 19th century biologists based the classification of whatever group they were studying in terms of the Biogenetic Law. It led some palaeontologists, such as Alpheus Hyatt, to select his ammonites and arrange them in evolutionary sequences to fit in with the Biogenetic Law, ignoring the stratigraphical data which showed no correspondence whatsoever.

But why did this powerful influence on biological thought for much of the 19th century seemingly just fade away into oblivion? Were Haeckel and his colleagues completely wrong? Is there no relationship between ontogeny and evolution? Or is the relationship different from that which the Haeckelian school perceived?

The demise of the relationship between ontogeny and evolution can be attributed to a number of factors. One was the publication in 1859 of Charles Darwin's 'Origin of Species', a book that shook the very foundations of both biology and theology. Most previous attempts to unravel the mysteries of the origins of species had been inward looking. They had concentrated on relationships intrinsic to the organism; to what was going on inside the organism as it developed. Darwin, on the other hand, changed the focus and looked at the extrinsic factors that affected why

particular species survived and others didn't: the role of competition; of the struggle between individuals; of the effect of the environment on selecting species.

Combined with this was the increasing number of examples in the fossil record where ontogeny didn't seem to be recapitulating phylogeny; it seemed that phylogeny was reversing ontogeny, with later forms resembling juveniles of their ancestors. But it took until the 1920's for someone to actually articulate what really appeared to be going on. That person was the marine biologist Walter Garstang, who studied tunicates (sea squirts), in particular their larvae. He argued (Garstang 1928) that vertebrates could have evolved from something as inconsequential as the larva of a sea squirt. This larva possesses all the attributes that one would expect in a vertebrate: a notochord; a dorsal hollow nerve chord; gill slits and a postanal propulsive tail. Garstang called this phenomenon of the retention of ancestral juvenile characters *paedomorphosis*—literally 'child shape'. He observed the same character in other groups of animals. For instance he noticed that there existed a number of salamanders that bred in water, and never metamorphosed into a terrestrial adult and retained a number of juvenile characters throughout their life. This is the poem that Garstang wrote, as he can describe it much more elegantly than I:

The Axolotl and the Ammocoete

*Amblystoma's a giant newt who rears in swampy waters,
As other newts are wont to do, a lot of fishy daughters:
These Axolotls, having gills, pursue a life aquatic,
But, when they should transform to newts, are naughty and erratic.*

*They change upon compulsion, if the water grows too foul,
For then they have to use their lungs, and go ashore to prowl;
But when a lake's attractive, nicely aired, and full of food,
They cling to youth perpetual, and rear a tadpole brood.*

*And newts Perennibranchiate have gone from bad to worse:
They think aquatic life is bliss, terrestrial a curse.
They do not even contemplate a change to suit the weather,
But live as tadpoles, breed as tadpoles, tadpoles altogether!*

Garstang effectively turned the Biogenetic Law upside down. However, this did not herald an upsurge in interest in the role of development in evolution. On the contrary. Few biologists had little faith left in the ability of the developmental history of an organism to tell us much about its evolutionary history. Two other factors combined to relegate such studies to the backwaters of biology. Firstly, there was the emergence of the study of genetics from the 1930s onwards. Second, was the most horrendous terminology ever perpetrated on mankind that arose from ontogenetic studies. Terms existed such as *paedomorphosis*, *peramorphosis*, *paedogenesis*, *progenesis*, *proterogenesis*, *palingenesis*, *pangeneses*, plus many more.

Fifteen years ago the American palaeontologist Stephen J. Gould published a book called 'Ontogeny and Phylogeny' in which he investigated the role of recapitulation and *paedomorphosis* in evolutionary theory. This book marked a renaissance in studies of the relationship between ontogeny and evolution, for what Gould (1977) argued was very simple. Haeckel and Garstang were both wrong, and they were both right. Recapitulation, in a very general sense, and *paedomorphosis* are both valid mechanisms for the generation of new morphologies. My own studies started in the 1970s at the time that Gould was writing his book, and our work, together with that of an increasing number of biologists and palaeontologists around the world has revealed that rather than being just a quaint evolutionary phenomenon, the study of the role of ontogeny in evolution is one of the cornerstones of evolution.

Indeed, it can be argued that it is the missing link in evolutionary studies. It is the link between genetics at one extreme and natural selection at the other, for it is the subtle changes in the rate and timing of development over countless generations that provides the raw materials on which natural selection can work.

In this address I propose to demonstrate countless examples of this phenomenon, to illustrate not only how it fits into current evolutionary theory, but also how it can explain the great diversity of life forms that exist on Earth today, and have existed since life evolved on this planet some 3.5 billion years ago. Without such changes to the rate and timing of development, life would not have evolved on this planet the way that it has.

Evolution means change—we think of it as the evolution of one species from another, or of one population of individuals from one another. Most people, I suspect, when they think about how living things have evolved probably think of how humans evolved from the apes, or how the animals and plants with which they are familiar came into being—but always from the viewpoint of adult animals or mature plants. Just picture any of the illustrations that have been used to chart the stately progression of *Australopithecus* to early species of *Homo*, through to *Homo sapiens*. Inevitably such illustrations depict adults (usually males), evolving from one into the other. But if we focus on the individual organisms—think about yourself if you like—then each organism undergoes a phenomenal degree of change from its moment of conception until it dies. You might think that there has been a dramatic change in appearance from an 'ape man', such as *Australopithecus*, to modern man. But this is nothing when compared with the morphological changes that occur as an individual of a single species develops.

Although your cognisant memory doesn't in reality allow it, let your imagination take you back to the time before you were born—go back to the first few days of your existence following conception. Think about what you looked like a few weeks after conception, the relatively enormous head and tiny limbs. Then you will realise the remarkable changes that you have undergone to get you to what you have become today. This is your ontogeny—your growth and development from embryo through juvenile to adult.

Now just consider for a moment what would happen if the orderly rate and timing of development of your bodily parts had been altered. If the rate at which a feature that changed mostly during the latter part of your juvenile development was slightly altered you might end up with a slightly longer leg, or perhaps shorter arm than usual. However, if a critical feature that formed early in your embryonic development, such as a limb bud, had perhaps started its growth either a little earlier or a little later than normal, or even not at all, then the consequences for your adult shape would have been tremendous.

This whole concept of changes to the timing and rate of development is known as *heterochrony* (literally 'changing time'). Basically the 'amount' of growth than an organism goes through during its ontogeny can be more than its ancestor or it can be less (Fig 1). This can apply to the organism as a whole, or to specific structures, like an arm, a leg, or whatever. More growth is known as *peramorphosis* (literally, 'beyond growth'). Less growth is known as *paedomorphosis*, as I mentioned earlier. Each of these states can be achieved in three basic ways (Alberch *et al.* 1979; McNamara 1986). A structure can start growth later than in the ancestor, but finish at the same time. This is known as *postdisplacement*. Alternatively an organism, or a

HETEROCHRONY

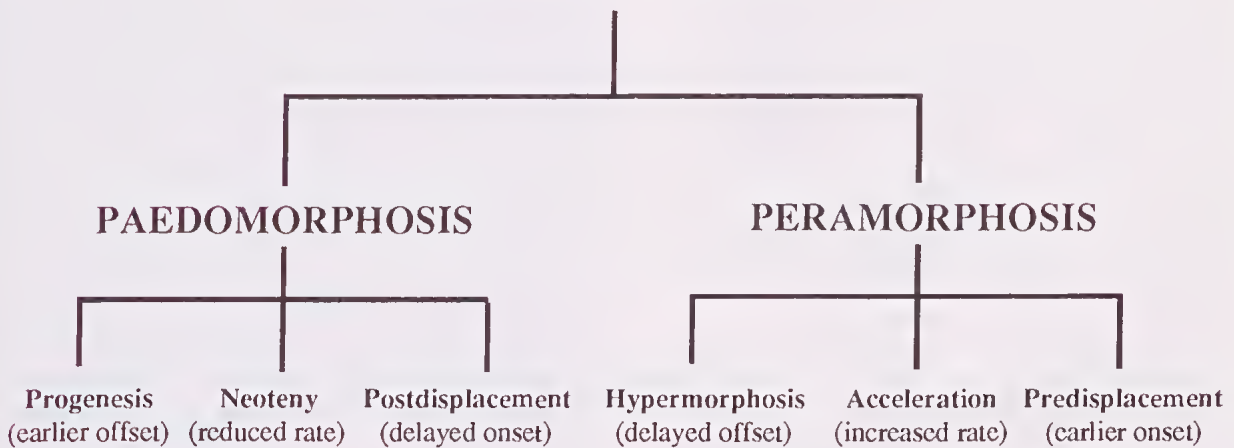


Figure 1. The hierarchical classification of heterochrony.

particular structure can grow at a slower rate than in the ancestor. This is known as *neoteny*. The last way to achieve paedomorphosis is for the organism, or part of the organism, to grow at the same rate as in the ancestor, but to finish growth earlier. This is known as *progenesis*.

The three ways to achieve *peramorphosis*, in other words, developing beyond the ancestor, are the opposite ways that paedomorphosis were achieved. Development can start earlier (*predisplacement*), and so get a head start; or it can go at a faster rate (*acceleration*), so developing further in the same time; or it can simply develop for a longer time and go farther (*hypermorphosis*), termination of growth being later than in the ancestor. These three pairs of mechanisms that target either the time of onset of development, its rate or its time of offset are the crux of heterochrony. And they can be used to explain much of the diversity of life.

Specific examples show how heterochrony operates within species; how it operates between species; how it can be affected by environmental factors; how it can be used in macroevolutionary studies to explain the evolution of major groups of organisms; how it demonstrates that natural selection may be targeting features other than an organism's morphology; how evolutionary trends can be explained; and illustrate how evolution affects the whole of an organism's life history.

Heterochrony within species

Let me take you gently into the world of heterochrony by introducing you to a character with which you are probably very familiar, but which you may not recognise at first—the early Snoopy. The cartoon character Charlie Brown's canine companion is immediately recognisable today as a dog that is largely all head, with diminutive limbs, and less than impressive body. But the very first Snoopy created some decades ago was quite different.

Here was a fairly typical, happy-go-lucky dog, long of limb and long of tooth and jaw, most unlike his evolved form we see in newspapers and comic books today. Now, consider how this prototype Snoopy changed as it grew from a cute, cuddly little puppy into a bundle of canine energy. The changes in shape that an average dog goes through from birth to adulthood are quite profound (see Wayne 1986). Apart from an increase in size, many of the

body proportions change quite appreciably. For instance the legs become relatively longer and the skull undergoes a great elongation, changing from a near-rounded shape in early juveniles, to a long muzzled shape in adults. Now, just imagine what would happen to our prototype Snoopy if it became sexually mature much earlier than its immediate ancestor, resulting in the premature cessation of growth. What would our dog look like? He would look like the Snoopy as we know him today—a paedomorphic dog.

While here we are dealing with what might be a subconscious desire on the part of the cartoonist to select for 'cuteness' (see Gould's [1979] similar analysis of the evolution of Mickey Mouse), a character that is of selective advantage to a juvenile dog, this is more than just a mere flippant example of the concept of heterochrony. Let us consider heterochrony in real dogs. The many and varied breeds of the domestic dog differ from each other largely in terms of body size and growth rate. Some, such as chihuahuas or King Charles spaniels, differ from an average dog by retaining, as adults, ancestral juvenile characters—they are paedomorphic in retaining a much smaller muzzle and a relatively large cranium. An Irish Wolfhound, on the other hand, is peramorphic, having gone "beyond" the ancestral dog in its degree of development, attaining a greatly prolonged muzzle (Fig 2). These major differences in the appearance of these breeds have an underlying genetic basis in the control of the rate and timing of production of growth hormones.

The underlying importance of this great change in growth proportions during ontogeny is shown by comparing the growth of a dog skull with that of a cat. In terms of overall body shape and proportions, dog breeds exhibit a far greater range than do breeds of cat (Wayne 1986). This arises from the much higher proportionate growth rate of the dog skull, particularly with regard to the length of the muzzle (Fig 3A,B). In cats, on the other hand, there are much lower proportionate growth changes (Fig 3C,D). There is thus a smaller range of variations to be selected from in cats, compared with dogs.

Environmental effects can act directly on certain members of a population to produce unusual growth forms by heterochrony. One such example is the effect that diet has on growth in the caterpillar *Pseudoeletia unipuncta*. Experiments of Berneys (1986) have shown that the proportionate size of the head can change, depending on the nature of the

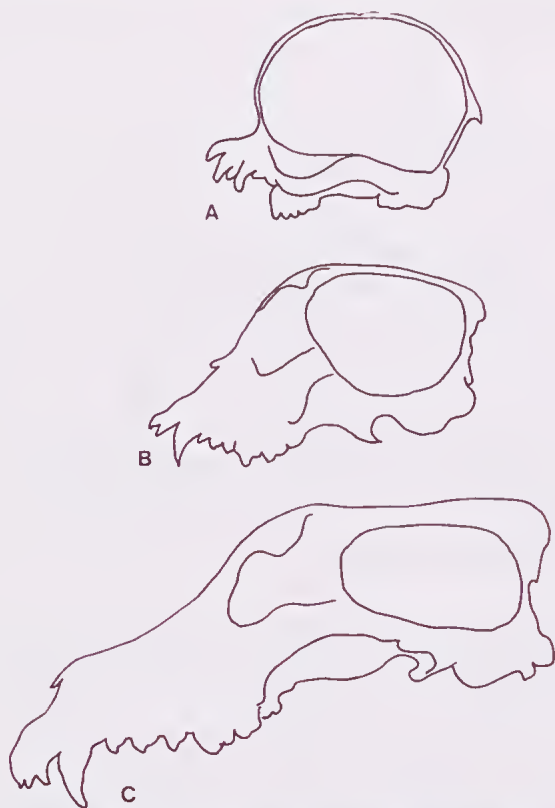


Figure 2. Transverse sagittal sections through skulls of adult dogs: A, King Charles spaniel; B, English bulldog; C, Irish Wolfhound. Compared with the bulldog, the spaniel is paedomorphic, and the wolfhound peramorphic. Redrawn from Weidenreich (1941).

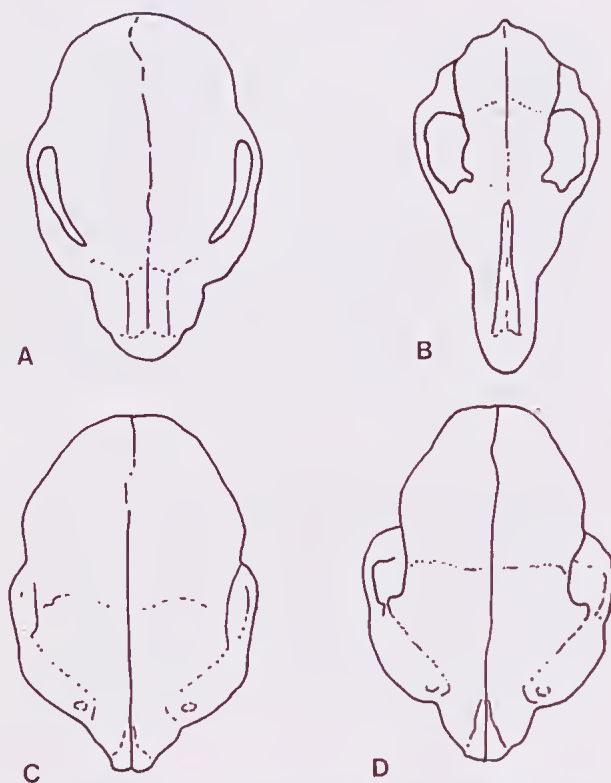


Figure 3. Dorsal view of skull of juvenile domestic dog (A) and adult dog (B), contrasted to that of juvenile domestic cat (C) and adult cat (D). Note the greater degree of morphological change during ontogeny of the dog skull compared with that of the cat. Skulls are normalised for size. Redrawn from Wayne (1986).

diet. Caterpillars fed on a diet of grass develop heads twice the mass of those fed a soft artificial diet. Those fed an intermediate diet developed an intermediate head size. These differences in overall head size have been attributed to increased muscular development. There is a genetic basis to these changes, for of 82 species of grasshoppers and 76 species of caterpillars from North America and Australia, grass eaters consistently have larger heads than herbaceous plant eaters. Here is an example of peramorphosis acting not on the whole organism but on one particular structure. I shall discuss later this "dissociation of parts".

Environmental factors such as temperature can also have a profound effect on what an organism looks like. This is well shown in some molluscs. For example, the Atlantic squid *Sthenoteuthis pteropus* occurs as three polymorphs: a small form, a medium form and a large form (Zuev *et al.* 1979). There is a direct correlation between maximum size reached and time of onset of maturity. There is also an inverse correlation between higher temperature and increasing size. Consequently the smallest forms of this squid occur in oceans with a water temperature between 26–30°C; large forms in water between 18–22°C (McKinney & McNamara 1991, Fig 4-4). The same phenomenon is exhibited by the Indo-Pacific squid *Sthenoteuthis oyalaensis*; early and later maturing males and females differ in final body size, the earlier maturing forms being restricted to warmer water. So, these forms can be considered as paedomorphic early finishers, or progenetic forms (Fig 1).

One of the classic examples of paedomorphosis occurs in the salamander known as an axolotl, or Mexican salamander. These salamanders' rate of morphological change is so reduced that it fails to metamorphose and so retains its larval gills, even when sexually mature. It also retains ancestral juvenile behavioural patterns by remaining in the juvenile aquatic environment and not metamorphosing into a land-dwelling form.

Such paedomorphosis is common in salamanders (Sprules 1974; Larson 1980; Alberch & Alberch 1981). Many different lineages show similar changes in morphology. In descendant species the tails become shorter, feet become fully webbed and the skulls are less bony, features of adult paedomorphic salamanders that occur in juveniles of their ancestors. Many of these paedomorphic species have a slower growth rate (neoteny). However, some finish development earlier (progenesis). So here we can see that paedomorphosis in one group of animals can be achieved by two quite different mechanisms.

One intriguing question is why some populations of salamanders include paedomorphic individuals while others do not. Harris (1987) investigated this by raising larvae of the salamander *Notophthalmus viridegens dorsalis* in tanks under different population densities. Those kept at low population densities (10/tank) became paedomorphic and stayed in the water and bred in a juvenile form, while those at high population density (40/tank) metamorphosed into immature land-dwelling salamanders. This seems to make evolutionary sense. In the wild as ponds dry up, so the population density would increase. Under such circumstances selection would favour those individuals that metamorphose into terrestrial salamanders and disperse.

But why should some groups of animals, such as salamanders, show such a common occurrence of paedomorphosis both today and in the fossil record? Theoretically there is no reason why paedomorphosis should occur any more often than peramorphosis. Perhaps the answer to the high frequency of paedomorphic salamanders lies in the size of their cells. The larger the cell, the more DNA it is

likely to hold. The amount of DNA in a cell is known as the 'genome size' or 'C-value'. It would seem that there is a negative correlation between genome size and developmental rate. Many salamanders have high C-values. Sessions and Larson (1987) analysed the C-value for 27 species of amphibians and found that those with larger cell volumes had a slower developmental rate than those with smaller cell volumes.

A similar situation is found in lungfishes, with modern day species having large C-values. It is known from morphological studies that modern species are paedomorphic when compared with their ancestors (Bemis 1984), which have a good fossil record dating back more than 350 million years to the Devonian. By analysing the size of bone cells over this period it can be demonstrated that there has been a general increase in cell size (Thomson 1972), corresponding to the paedomorphic morphological changes that have been documented.

Heterochrony can produce not only shape but also size changes. Shorten the period of juvenile growth of an organism (progenesis) and it will not grow as large as its ancestor. Conversely, lengthen the growth period (hyper-morphosis) and the organism will grow larger. Many species, such as some ants, possess polymorphs of different sizes. Likewise many species exhibit sexual dimorphism. This, more often than not, is manifested in differences in size between males and females. Such differences are often caused by variations between polymorphs, or between sexual dimorphs, in the timing of cessation of growth i.e. differences in the timing of onset of sexual maturity.

Arguably the most extreme form of sexual dimorphism, and one that vividly illustrates the difference in degree of morphological development between sexes, occurs in an obscure group of gastropods, known as eulimids. In these genera such as *Entocolax*, *Entoconcha*, *Thyonicola* and *Enteroxenos*, the females live as parasites within holothurians, otherwise known as sea cucumbers. For many years it was thought that many of these species were hermaphrodites, until it was realised that what had been interpreted as the testes was in fact the entire male animal (Lützen 1968). The male lives within the female, entering her through the ciliated tubule that connects the female to its host's esophagus. The minute male attaches itself to a special receptacle within the female's body, where it grows into what is essentially little more than a testis (Fig 4). Such dimorphism, with a smaller paedomorphic male living within or upon the female, is not uncommon in invertebrates, particularly among molluscs and echinoderms.

Although similar extreme examples are not common in vertebrates they do occur. Perhaps the best known is the deep-sea angler fish *Photocorynus*. In this fish the male is very much smaller than the female and lives parasitically attached to the female's head. While the female reaches lengths of about one metre, the male is rarely longer than 15 cm. A recently described example (Hutchins 1992) is almost as stunning. The females of some species of leatherjackets much more closely resemble the juveniles in body shape than the males because the males have undergone a greater degree of ontogenetic change. Whether this is because males mature later than the females or whether they have accelerated growth is not known. There are also substantial differences in the skeleton between the male and female, again the female resembling the juvenile. Hutchins considers that a consequence of the difference in fin shape between the male and female explains differences between the two in the way that they swim. Developmental changes can induce behavioural differences too.

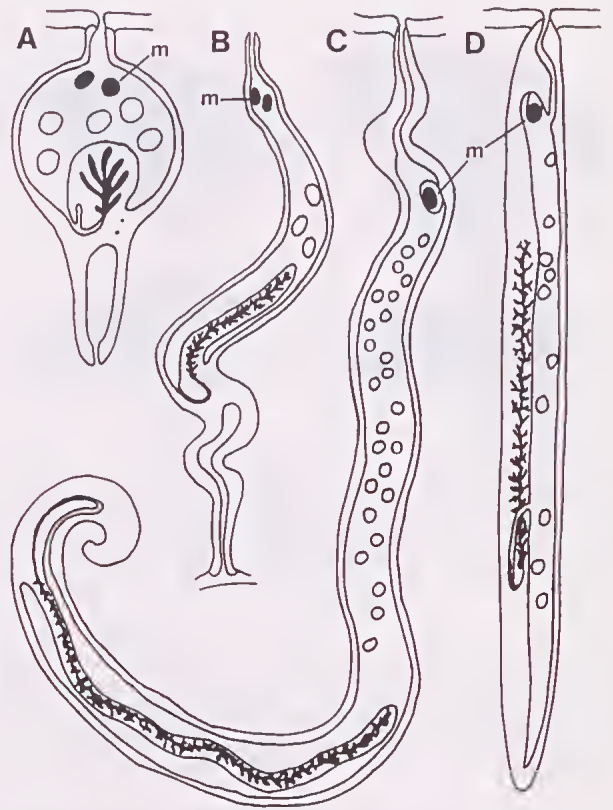


Figure 4. Extreme sexual dimorphism in eulimid gastropods, endoparasitic in holothurians. The progenetic male (m) lives within the female. A, *Entocolax*; B, *Entoconcha*; C, *Thyonicola*; D, *Enteroxenos*. Redrawn from Lützen (1968).

Heterochrony between species

The vast majority of differences between species in all groups of organisms are caused by changes to the timing and rate of development. We can try applying some of the principles of heterochrony to one of the classic examples of evolution—Darwin's Galapagos finches (Fig 5). Hitherto this classic example of evolution has been looked at purely from a natural selection point of view. I would like to look at it from the inside—from the point of view of structural changes that have taken place in the evolution of particular species to allow the adaptation to differing feeding habits.

The Galapagos finches show a wide variation in bill shape. These have allowed a wide range of food types to be utilised. Some bills are used for crushing, mainly different types of seeds; others are for probing; others for grasping and biting, predominantly insects. Such adaptations are often interpreted as having evolved "in order for the species to feed on a particular object", as though natural variation would only allow a particular bill shape to evolve if the necessary food was available. This "cart before the horse" approach ignores the role of heterochrony in the evolution of these bills. Because of these subtle changes to the growth rates of upper and lower beaks a wide range of morphotypes has evolved. Thus upper beaks that have increased their relative growth rate did so by peramorphosis, whereas those that underwent reduced growth rate are paedomorphic. This combination of heterochronic styles is known as dissociated heterochrony. Only if suitable food sources were available which could be exploited by a particular bill shape would this shape be selected for. The source of variation behind such evolutionary radiations is



Figure 5. Heads of four species of Galapagos finches, showing variation in bill shape and size. 1. *Geospiza magnirostris*; 2. *Geospiza fortis*; 3. *Geospiza parvula*; 4. *Certhidea olivacea*. Reproduced from Darwin (1839).

heterochrony arising from internal factors, rather than the external pressure of natural selection. This does not argue against natural selection. Two factors must operate in tandem; evolution is the product of both intrinsic and extrinsic factors.

Dissociated heterochrony can also be used to explain the macroevolution of some groups of birds. In particular the ratites, or flightless birds, such as the emu, ostrich, rhea and the extinct moa and aepyornis. De Beer (1956) claimed that flightless birds such as these were classic examples of the power of paedomorphosis to give rise to whole, new groups of animals. He argued that the very reduced wings and poorly developed breast bone showed that the ratites were paedomorphic birds. While not denying that these features are paedomorphic, I would argue that the characters selected for in ratites were not the the paedomorphic features, but two other features: the large body size, combined with the peramorphic legs. These, after all, are two important features of the ratites, without which they would not survive.

There is no doubt that ground dwelling birds are highly susceptible to predation. Just consider the fate of the dodo on Mauritius, the moa on New Zealand and the aepyornis on Madagascar. The reason for the possession of some paedomorphic features by these birds is that they were a necessary consequence of the selection for the peramorphic features. One was a trade off against the other. Just imagine what size wings an ostrich would require to get off the ground. Early Tertiary flightless birds, which were in fact the first large predators to exploit the niches vacated by dinosaurs, evolved enormous, powerful heads by peramorphosis. But they too would have evolved from flying birds and have also suffered paedomorphic reduction in wing size.

Probably the most important message to emerge from heterochronic studies in the last decade is the fact that not only do both paedomorphosis and peramorphosis occur but that most organisms are a product of these two opposing forces. And if you consider the number of morphological features in an organism that can have their growth trajectories altered, you will quickly realise that the potential combinations that can evolve is mathematically enormous. While many of these combinations would probably not be functionally possible, the diversity of life on this planet is testimony to the power of heterochrony to generate a sufficient diversity of successful forms.

Although there has been much less research on the role of heterochrony in plants, what has been done is showing that heterochrony operates equally well in plants (Guerrant 1988). From an Australian perspective Carpenter (1991) has stressed the importance of heterochrony in the evolution of the cycad *Macrozamia*, while recent work by Wiltshire *et al.* (1991) on some species of *Eucalyptus* has demonstrated the importance of paedomorphosis in leaf and fruit development.

Dissociated heterochrony figures as prominently in plants as it does in animals. Take for example the *Delphinium*. A study by Guerrant (1982) focused on *Delphinium nudicaule*, a species which is pollinated by hummingbirds. The external appearance of the flowers results from a reduced rate of development of the floral parts, producing a paedomorphic morphology. For example, the sepals face forward, as they do in the bud. This produces a tubular flower characteristic of plants pollinated by hummingbirds. Not all of the plant's features are paedomorphic, however. The petals, unlike the sepals, develop faster, which results in a shape beyond that of the generalised delphinium. So selection acting on the development of the flower in different ways, retarding some features, accelerating others, produced a new shape capable of attracting and rewarding a new pollinator. This was a major adaptive breakthrough for the plant, that didn't involve dramatic genetic changes.

Heterochrony and selection for body size

Many examples show selection acts on the shape of particular structures, but selection may be acting on other aspects of developmental change. There is one particular mechanism that either extends the period of growth or reduces the period of growth. The two resultant effects, progenesis for reduced growth, and hypermorphosis for extended growth, produce not only shape changes but also size changes. Reducing the juvenile phase of growth results in the evolution of a smaller adult body size than possessed by the ancestor; extending the growth period produces a larger adult.

The fossil record demonstrates many examples of evolutionary trends of increased body size (McKinney 1990). Such trends are so common that they have been codified as Cope's law. Heterochrony has been used to explain some of these size increases, for instance in titanotheres (McKinney & Schoch 1985) and the Irish Elk (Gould 1974; Fig 6). Here I will demonstrate this with two examples, one of which is also a classic evolutionary example—the evolution of horses. Recent analysis of the evolution of horses shows that rather than being a simple evolutionary trend leading from small browsing forms in the early Tertiary to larger grazers in the later Tertiary, there was a great complex of forms, which show an overall trend towards selection for larger body size (MacFadden 1986). Traditionally, the evolution of horses has been shown to be dominated by changes to the form of the foot, with an overall, paedomorphic reduction in the number of toes, and a change in the shape of the teeth that allowed a change from a browsing to a grazing habit. Many of the changes may be considered to be, in part, by-products of the selection for increased body size. Thus delay in onset of maturity will have allowed a larger body size to be attained, and this in turn will have dragged along proportionate changes in certain structures, such as the form of the teeth and legs.



Figure 6. The Irish Elk, *Megaloceros giganteus*. Although not confined to Ireland, nor an elk, this deer has been cited (e.g. Gould 1974) as a classic example of hypermorphosis, the large antlers being interpreted as a by-product of selection for large body size.

Another example is in dinosaurs. Early triceratopsians were small creatures, not the lumbering hulks that existed in the late Cretaceous. As a consequence, structures such as the large horns present on the head found in later large forms, were barely developed in early small forms (Fig 7). Selection for a larger body size resulted in structures such as these being also developed. The question to answer when attempting to interpret such trends is which factor was under strongest selection pressure: body size, or specific morphological features, such as the horns? It may have been that in the triceratopsians, even though primary selection was on body size, perhaps as a means of combating predation pressure, there was added benefit in that extension of the growth period allowed structures such as the horns to increase greatly in relative size.

Evolution is not always towards increasing complexity and larger size. Many small species of animals and plants are likely to have evolved from larger ancestors by heterochronic mechanisms, such as precocious onset of maturity (progenesis). For example, many small species of trilobites in the fossil record are thought to have evolved in this way (McNamara 1983). Although adults, they retain ancestral juvenile features, such as fewer body segments, and a small body size (Fig 8). The question that again must be asked is, what was selection acting upon: was it the particular morphological features attendant on the small size? Was it the small size itself? Or was it some other factor, and both shape changes and body size changes were a by-product of selection for some other factor?

Heterochrony and the selection of life history strategies

Classic life history strategy studies identify a continuum between forms that inhabit unstable environments where selection favours small forms, with short life spans, reproduce frequently and have large numbers of offspring (sometimes known as *r*-selected forms), and forms that inhabit stable environments, and have large body size, long

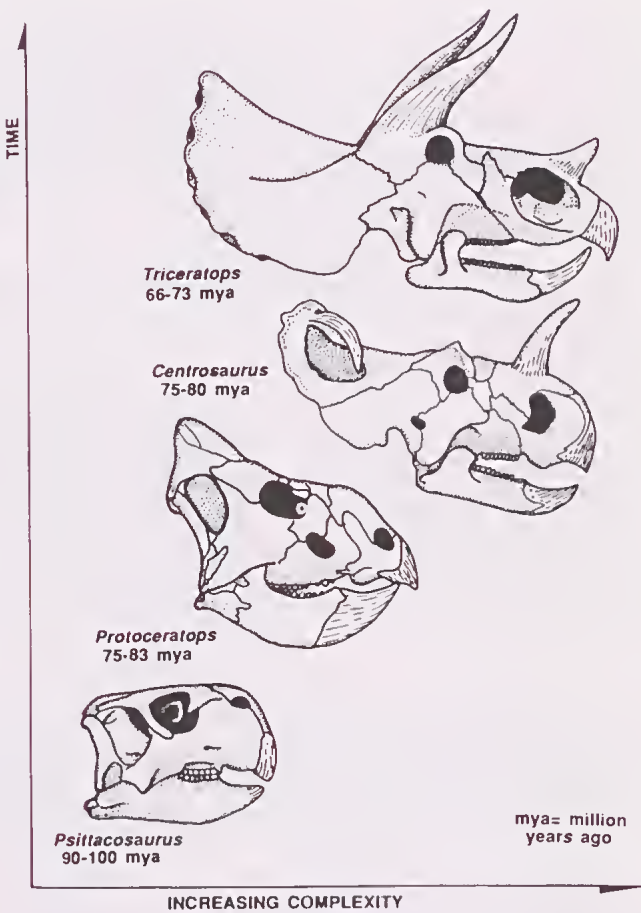


Figure 7. Evolution of the skull of triceratopsian dinosaurs, showing that as they increased in size, so horns and bone frills became more ornate. Later species are much larger than earlier species. Reproduced, with permission, from Long (1992).

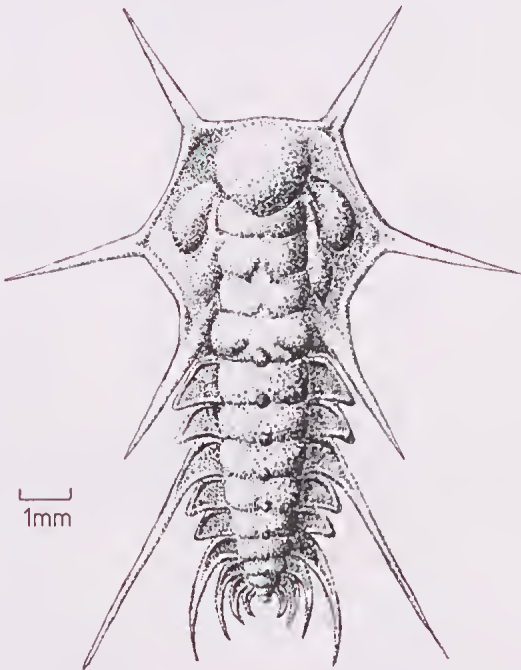


Figure 8. *Olenelloides armatus*, a progenetic trilobite from the early Cambrian of Scotland. Reproduced, with permission, from McNamara (1978).

life spans and reproduce infrequently with small numbers of offspring (sometimes known as *K*-selected forms). Let us consider some of these features of the two extreme forms. The small body size and short life span of those living in unstable, ephemeral environments corresponds to our "early finishers" or progenetic forms, that I have discussed earlier. The large body size and long life span of the other extreme are characteristic of the "late finishers", or hyper-morphic forms.

Hafner and Hafner (1988) have looked at heterochrony in some species of kangaroo mouse and kangaroo rats from North America in terms of life history strategies and have presented a very elegant model that shows how selection did not favour the length of the mouse's tail or the colour of its fur, or the size of its eyes, but the actual life history strategy of the animal. The morphological features that evolved were certainly not maladaptive to the animals, and must have also been of some adaptive significance. But the fact that one species might have a slightly longer tail than another shouldn't be explained in terms of what adaptive advantage this conferred to the species. It would merely have been a by-product of selection for some particular life style.

It had long been argued that the possession by these heteromyid rodents of features such as enormous head, huge hind feet, large eyes and long tail were all specific adaptations to living in a desert. The argument went that the large head counterbalanced the rodent as it hopped purposively through the cool desert night on its huge sand-paddle feet, searching for food with its big eyes and steering with its rudder-like tail. Not so, argue the Hafners. The small size and retention of ancestral juvenile traits by the adult kangaroo mouse *Microdipodops* is likely to have arisen because of early onset of maturity producing a mouse with a body length less than 8 cm. The adult of the larger kangaroo rat, *Dipodomys*, has similar ancestral juvenile characters, but these evolved by a reduction in the rate of development. This rat is much larger than the kangaroo mouse, with a body up to 20cm long. It has a longer life span, slower development, longer gestation period and smaller litters than the mouse. These are the features that were being selected for—not the fact that it might have had a few more whiskers, or slightly longer tail.

Another related rodent is a large pocket gopher that grows to more than a third of a metre in length. Here, rather than retardation in development, there has been an extension of development by a delay in the onset of maturity. This produced a large, robust animal. Its longer life span that produced these morphological features, is associated with a life history strategy like that of the kangaroo rat: small litter size and long gestation period.

Perhaps the most extreme example of the interrelationship between life history strategy and heterochrony is one where there is very little morphological separation between forms, but profound variation in time of maturation. And it has all happened over just the last 200 years in the apple maggot fly, *Rhagoletis pomonella*, which has evolved a number of races that are adapted to feeding from a range of trees (Feder *et al.* 1988; McPherson *et al.* 1988; Smith 1988; Barton *et al.* 1988). Originally adapted to feeding from hawthorn trees in North America this fly has spread to infest trees such as apples, cherries, roses and pears. Behaviourally, offspring of a fly from, say, an apple tree, are more likely to lay their eggs on other apple trees. There are significant differences in the timing of onset of maturity of the fly on different hosts. Under laboratory conditions the "ancestral" hawthorn fly takes between 68 and 75 days to mature. The apple fly takes only 45-49 days. Flies that

infest fruit of the dogwood, however, take between 85 and 93 days. The onset of maturation varies because it is timed to coincide with the period of maturation of the fruit of the host tree (Table 1). The result of this has been not only the establishment of behavioural barriers to gene flow but also developmental barriers, as mating time of the flies from different hosts will vary.

Table 1

Variations in timing of onset of maturity and its relationship to time of fruit maturation in races of the apple maggot fly *Rhagoletis pomonella*. Data from Feder *et al.* (1988), McPherson *et al.* (1988) and Smith (1988)

Host	Days to Maturity	Fruit Maturation Time
Hawthorn trees	68-75	early autumn
Apple trees	45-49	mid-late summer
Dogwood trees	85-93	mid-late autumn

Heterochrony and predation pressure

While heterochrony provides the fuel for evolution, what actually drives evolution along? Why are particular shapes and size evolved and not others? One important aspect that is emerging from this work is the realisation that many evolutionary trends, such as the evolution of horses, are constrained by developmental changes. But why do the trends go in the direction that they do. What is driving them along? The fossil record is replete with examples of such evolutionary trends (McNamara 1988, 1990a), and some are providing indications that predation pressure is a potent force in selecting for particular shapes and sizes. Let me briefly demonstrate one example from the fossil record, then two from living animals.

Many of the evolutionary trends in sea urchins that have been documented from the fossil record in southern Australia parallel evolution of the lineages from shallow to deep water environments over a period of about 40 million years (McNamara 1990b). These urchins are a group known as heart urchins, most of which burrow into the sediment. To evolve from living in coarse sands in shallow water to inhabiting fine sands and muds in deep water necessitates the evolution of particular structures. While many of these heart urchins have lost the long sharp spines characteristic of urchins that roam reef platforms, a few possess a small number on their dorsal surface which have been shown to possess a defensive function.

One lineage of the urchin *Lovenia* shows how the number and distribution of dorsal spines varied from the earliest 20 million year old species through another species that lived 15 million years ago, to the last of the lineage that lived about 10 million years ago. The areas of the urchin's shell covered by these spines progressively decreased along the lineage by pedomorphosis (Fig 9) as the urchin evolved into finer sediments deposited in deeper water (McNamara 1989, Fig 7; McNamara 1990b, Fig 9.9). The spines on the ventral surface of *Lovenia*, however, like those in many other heart urchins, are adapted for digging into the sand. These increased in concentration by peramorphosis along the lineage. A greater concentration of such spines would have been a prerequisite for digging in finer sands.

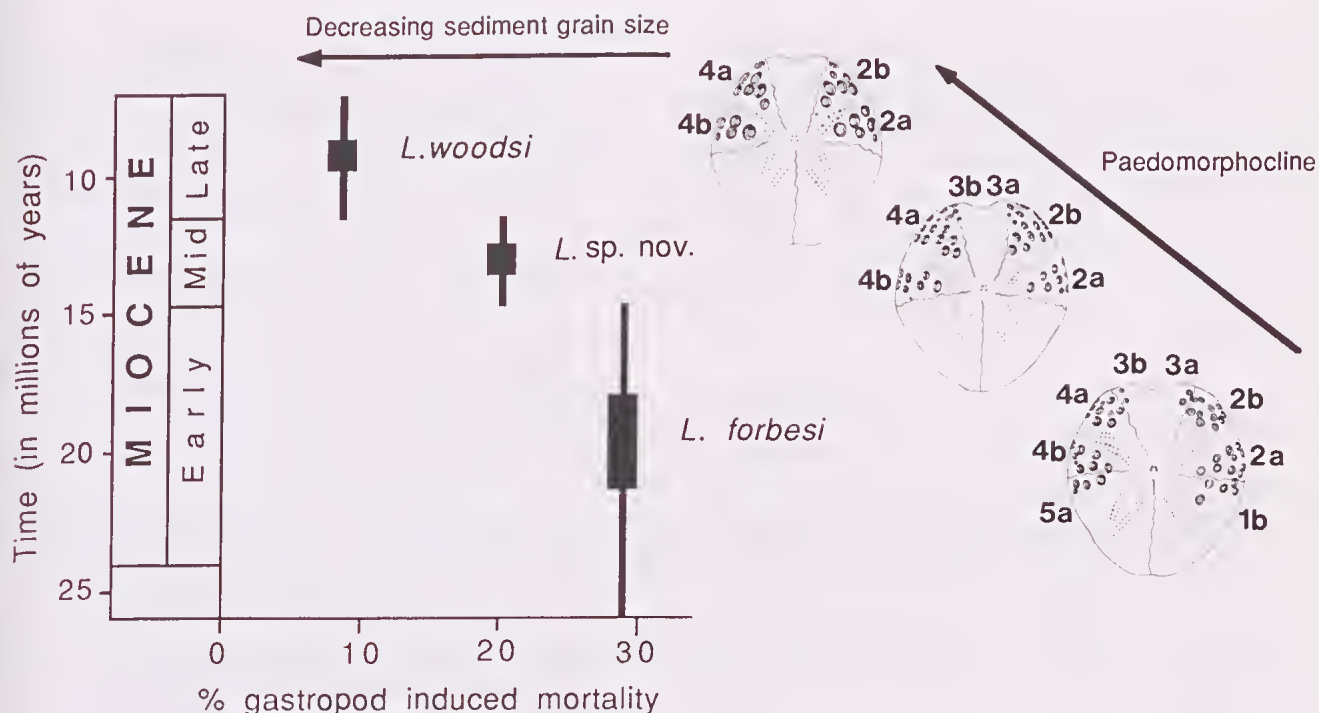


Figure 9. Gastropod induced mortality through time in three Australian species of the heart urchin *Lovenia* showing selection for forms with paedomorphically reduced dorsal spines in regions of lower predation pressure. Reproduced, with permission, from McNamara (1990b).

Many of the urchin fossils bear a small hole in their test, rather like a small bullet hole. These holes were cut by predatory cassid gastropods. By analysing the frequency of occurrence of lethal predation it can be shown that gastropod-induced mortality was nearly 30% in the shallowest water species, that lived in the Early Miocene; 20% in the deeper water intermediate Middle Miocene species, and only 8% in the deepest water species, the last in the lineage that occurred in the Late Miocene (Fig 9). Cassid gastropods are known today to occur with highest frequency in shallow water, and decrease in diversity into deeper water. I would suggest that the high level of predation on these urchins in shallow water was the driving force that directed their evolution, by selection of forms with particular developmental rates, that were better adapted to living in deeper water, where there were fewer predators.

A similar effect can be demonstrated in some living animals. For instance the three-spined stickleback fish *Gasterosteus* shows paedomorphic pelvic reduction that is induced directly by predation pressure (Bell 1988). During development, the pelvic girdle grows to become a prominent spine in forms that live in the sea. In this environment the main predators are other fishes that try to swallow the stickleback whole. A stout spinose pelvic girdle is an effective deterrent to such predators. However, in freshwater habitats there is a shift in the type of predator away from fish to insects. Whereas the pelvic spines are useful armour against other fish they are maladaptive in freshwater because predatory insects use them to grip onto the small fish. Selection pressure in the freshwater environment favours those sticklebacks that reduced the amount of growth of the pelvic spine. There is evidence from the fossil record that such pelvic reduction in sticklebacks is heritable. In a 110,000 year sequence in Miocene rocks pelvic reduction is observed to have occurred (Bell 1988). With the reduction in pelvic spines there was a reduction and then ultimate disappearance of all other fishes from the sequence, indicating that vertebrate predators had gone, replaced, perhaps by invertebrate predators.

Recent work on the freshwater snail *Physella virgata* (Crowl & Covich 1990) has shown that timing of growth and thus shell size can be directly influenced by the presence or absence of predatory crayfish. Populations free from the predator show rapid growth until a shell length of about 4mm, at which time reproduction begins and growth rate declines. The snails live for 3 to 5 months. Introduce a predator into the system in the form of a crayfish and the snails delay their onset of maturity, and so achieve a larger size. As a consequence, individuals live longer. As the crayfish prey preferentially on small snails it is to the snail's advantage to grow to a larger size as rapidly as possible. This switch in the timing of maturation in the snail is caused by a chemical cue introduced by the crayfish.

Conclusions

This brief tour through elements of the animal and plant kingdoms has illustrated the importance of variations to the timing and rate of development in evolution. It is fitting to conclude this address with a final species—*Homo sapiens*. If heterochrony has been so influential in the evolution of so many animals and plants, then there is no reason why it should not also have played an important role in human evolution. Just think of any illustrations in textbooks of hominid evolution: they are invariably portrayed purely in terms of the evolution of adults. But I believe that the whole of the period of development must be investigated to understand fully how humans evolved.

The Dutch anatomist Loius Bolk observed (Bolk 1926) that adult humans possess many features present in juvenile apes, such as flat faces, reduced body hair, relatively large brains housed in thin skull bones, absence of brow ridges and a cranial crest and small teeth that erupt later in life. While there may be a few people you know who resemble adult apes, I'm sure that most would more closely resemble the juvenile (see Gould 1977, Fig 61). However recent work, particularly by Shea (1988) and

McKinney & McNamara (1991), suggests that some of these apparent paedomorphic characters might be overshadowing other developmental changes that have occurred in hominid evolution. There are a number of important characters possessed by adult humans that do not occur in juvenile apes. For example the structure of the base of the skull, which allows us to walk upright and face forward, bears no resemblance to that of a juvenile ape. But most significant is our overall size and our large brain. These are not the product of retarded development. On the contrary they are the product of peramorphosis resulting from our delayed onset of maturity (hypermorphosis), compared with other apes.

We are the late finishers among the primates in terms of our period of extended juvenile growth. Our prolonged period as juveniles has resulted not only in us attaining a larger body size than our ancestors, but also, importantly, a larger brain. Significantly this allowed a longer period in the critical phase of learning. Certainly, like the delphinium flower, we are the product of dissociated heterochrony: some parts of our anatomies are retarded, while others have developed beyond those of our ancestors. But arguably it is these hypermorphic, prolonged features that were the ones that led to the success of our species on this planet, and all that that has entailed.

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References

- Alberch P & Alberch J 1981 Heterochronic mechanisms of morphological diversification and evolutionary change in the neotropical salamander, *Bolitoglossa occidentalis*. *Journal of Morphology* 167:249-264.
- Alberch P, Gould S J, Oster G F & Wake D B 1979 Size and shape in ontogeny and phylogeny. *Paleobiology* 5:296-317.
- Barton N H, Jones J S & Mallet J 1988 No barriers to speciation. *Nature* 336:13-14.
- Bell M A 1988 Stickleback fishes: bridging the gap between population biology and paleobiology. *Trends in Ecology and Evolution* 3:320-325.
- Bemis W E 1984 Paedomorphosis and the evolution of the Dipnoi. *Paleobiology* 10:293-307.
- Berneys E A 1986 Diet-induced head allometry among foliage-chewing insects and its importance for graminivores. *Science* 231:495-497.
- Bolk L 1926 *Problem der Menschwerdung*. Fischer, Jena.
- Carpenter R J 1991 *Macrozamia* from the Early Tertiary of Tasmania and a study of the cuticles of extant species. *Australian Systematic Botany* 4:433-444.
- Crowl T A & Covich A P 1990 Predator-induced life-history shifts in a freshwater snail. *Science* 247:949-951.
- Darwin C 1839 *Journal of researches into the geology and natural history of the various countries visited by HMS Beagle*. John Murray, London.
- De Beer G 1956 The evolution of ratites. *Bulletin of the British Museum (Natural History) Zoology* 4:59-70.
- Feder J L, Chilcore C A & Bosh G L 1988 Genetic differentiation between sympatric host races of the apple maggot fly *Rhagoletis pomonella*. *Nature* 336:61-64.
- Garstang W 1928 The morphology of the Tunicata, and its bearing on the phylogeny of the Chordata. *Quarterly Journal of Microscopical Science* 75:151-187.
- Gould S J 1974 The evolutionary significance of 'bizarre' structures: antler size and skull size in the 'Irish Elk' *Megaloceros giganteus*. *Evolution* 28:191-220.
- Gould S J 1977 *Ontogeny and Phylogeny*. Harvard University Press, Cambridge.
- Gould S J 1979 A biological homage to Micky Mouse. *Natural History* 88:30-36.
- Guerrant E O 1982 Neotenic evolution of *Delphinium nudicaule* (Ranunculaceae): a hummingbird-pollinated larkspur. *Evolution* 36:699-712.
- Guerrant E O 1988 Heterochrony in plants: the intersection of evolution, ecology and ontogeny. In: *Heterochrony in Evolution: A Multidisciplinary Approach* (ed M L McKinney). Plenum, New York, 111-133.
- Hafner J C & Hafner M S 1988 Heterochrony in rodents. In: *Heterochrony in Evolution: A Multidisciplinary Approach* (ed M L McKinney). Plenum, New York, 217-235.
- Harris R N 1987 Density-dependant paedomorphosis in the salamander *Notophthalmus viridescens dorsalis*. *Ecology* 68:705-712.
- Hutchins J B 1992 Sexual dimorphism in the osteology and myology of monacanthid fishes. *Records of the Western Australian Museum* 15: 739-747.
- Larson A 1980 Paedomorphosis in relation to rates of morphological and molecular evolution in the salamander *Ambystoma flavipunctatus* (Amphibia, Plethodontidae). *Evolution* 34:1-17.
- Long D M 1992 *An Introduction to Dinosaurs*. Dragonglass, Perth.
- Lötzen J 1968, Unisexuality in the parasitic family Eutoconchidae (Gastropoda: Prosobranchia). *Malacologia* 7:7-15.
- MacFadden B J 1986 Fossil horses from "Eohippos" (*Hyracotherium*) to *Equus*: scaling, Cope's Law, and the evolution of body size. *Paleobiology* 12:355-369.
- McKinney M L 1990 Trends in body size evolution. In: *Evolutionary Trends* (ed K J McNamara). Belhaven, London, 75-118.
- McKinney M L & Schoch R M 1985 Titanotheres allometry, heterochrony, and biomechanics: revising an evolutionary classic. *Evolution* 39:1352-1363.
- McKinney M L & McNamara K J 1991 *Heterochrony: the Evolution of Ontogeny*. Plenum, New York.
- McNamara K J 1978 Paedomorphosis in Scottish olenellid trilobites (early Cambrian). *Palaeontology* 21:635-655.
- McNamara K J 1983 Progenesis in trilobites. In: *Trilobites and Other Early Arthropods: Papers in Honour of Professor H.B. Whittington, FRS* (eds D E G Briggs & P D Lane), Special Papers in Palaeontology 30:59-68.
- McNamara K J 1986 A guide to the nomenclature of heterochrony. *Journal of Paleontology* 60: 4-13.
- McNamara K J 1988 The abundance of heterochrony in the fossil record. In: *Heterochrony in Evolution: A Multidisciplinary Approach* (ed M L McKinney). Plenum, New York, 287-325.
- McNamara K J 1989 The role of heterochrony in the evolution of spatangoid echinoids. *Geobios, mémoire spécial* 12:283-295.
- McNamara K J 1990a *Evolutionary Trends*. Belhaven Press, London.
- McNamara K J 1990b Echinoids. In: *Evolutionary Trends* (ed K J McNamara). Belhaven Press, London, 205-231.
- McPherson B A, Smith D C & Berlocher S H 1988 Genetic differences between host races of *Rhagoletis pomonella*. *Nature* 336: 64-66.
- Sessions S K & Larson A 1987 Developmental correlates of genome size in plethodontid salamanders and their implications for genome evolution. *Evolution* 41:1239-1251.
- Shea B T 1988 Heterochrony in primates. In: *Heterochrony in Evolution: A Multidisciplinary Approach* (ed M L McKinney). Plenum, New York, 237-266.
- Smith D C 1988 Heritable divergence of *Rhagoletis pomonella* host races by seasonal asynchrony. *Nature* 336:66-67.
- Sproles W G 1974 The adaptive significance of paedogenesis in North American species of *Ambystoma* (Amphibia: Caudata): an hypothesis. *Canadian Journal of Zoology* 52:393-400.
- Thomson K S 1972 Estimation of cell size and DNA content in fossil fishes and amphibians. *Journal of Experimental Zoology* 205:315-320.
- Wayne R K 1986 Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution* 40:243-261.
- Weidenreich F 1941 The brain and its role in the phylogenetic transformation of the human skull. *Transactions of the American Philosophical Society* 31: 321-442.
- Wiltshire R J E, Potts B M & Reid J B 1991 A paedomorphocline in *Eucalyptus*: natural variation in the *E. risdonii/E. tenuiramis* complex. *Australian Journal of Botany* 39:545-566.
- Zuev G, Nigmatullin C M & Nikolsky V N 1979 Growth and life span of *Stenoteuthis pteropus* in the east-central Atlantic [In Russian]. *Zoological Zhurnal* 58:1632-1641.

Stratigraphy of the Lefroy and Cowan palaeodrainages, Western Australia

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Abstract

This paper revises the stratigraphy of the Lefroy and Cowan palaeodrainages, and compares it with that of the Eucla and Bremer Basins. The definition of the Eundynie Group is modified, and the terms Redmine Group, Revenge Formation, Gamma Island Formation, Polar Bear Formation, Roysalt Formation, and Beta Island Member are proposed.

The Eocene palaeodrainage succession is placed in the Eundynie Group, and the post-Eocene succession in the Redmine Group. The Eundynie Group in the Lefroy Palaeodrainage consists of the non-marine to marginal marine Hampton Sandstone and Pidinga Formation, and Princess Royal Spongolite. In the Cowan Palaeodrainage, the Eundynie Group consists of the Werillup Formation, Norseman Limestone, and Princess Royal Spongolite. The Redmine Group consists principally of the clastic Revenge Formation. Carbonate units within the Redmine Group comprise the Cowan Dolomite in Lake Cowan (formerly placed in the Eundynie Group) and the Gamma Island Formation in Lake Lefroy. These formations are of probable Miocene age. Pliocene and younger evaporites are named the Roysalt and Polar Bear Formations in Lakes Lefroy and Cowan respectively. Gypsum dunes on Lake Lefroy comprise the Beta Island Member of the Roysalt Formation.

Introduction

Chains of linear playa lakes are a prominent physiographic feature of the Kambalda and Norseman area (Fig 1). The subject of investigation since Woodward (1897), these lake chains are interpreted as the remnants of palaeodrainage systems as first proposed by Gibson (1909). Little published data exists on the sediments in the palaeodrainages.

Recent drilling by Western Mining Corporation (WMC) during exploration for Archaean gold and nickel deposits has provided data on the stratigraphy of the Lefroy and Cowan palaeodrainages. These data allow the resolution of the relationship between the marginal stratigraphy of the Eucla and Bremer Basins.

The aim of this paper is to describe the stratigraphy of Lakes Lefroy, Cowan, and Dundas and their adjacent areas; revise the definition of the Eundynie Group (Cockbain 1968a); introduce the new terms Redmine Group, Revenge, Gamma Island, Polar Bear and Roysalt Formations, and Beta Island Member; and clarify stratigraphic relationships along the boundary of the Eucla and Bremer Basins. The sedimentary facies and evolution of the palaeodrainage fill are the subject of a separate paper (Clarke in press).

The paper is based of geomorphological mapping the Lake Lefroy area, logging of percussion diamond and air-core drill holes, and petrography. Palynological analysis of organic rich samples provided biostratigraphic control.

Regional Setting

Lakes Lefroy, Cowan, and Dundas occur in the south-eastern part of the Archaean Yilgarn Craton, and are within the palaeodrainage network defined by Bunting *et al.* (1974) and Van de Graaff *et al.* (1977). Lake Lefroy occurs within the Lefroy palaeodrainage, and Lakes Cowan and Dundas occur in the Cowan palaeodrainage. The bedrock surface beneath the lake surface defines a V-shaped palaeovalley (Figure 2).

Stratigraphy

Eundynie Group

The presence of Tertiary marine sediments in the Norseman and Lake Dundas region has been recognised since early this century (Campbell 1906). They have not previously been reported from beneath Lake Lefroy, although they are known from further east (Griffin 1989). The only outcrops of marine sediments in Lake Lefroy occur near Loves Find (Locality 7, Figure 1).

Eocene carbonates and spongolites in Lake Cowan were termed the Eundynie Group (Figure 3) by Cockbain (1968a). The usage is here expanded to include all Eocene sediments in palaeodrainages marginal to the Eucla and Bremer Basins. The Eundynie Group is thus laterally equivalent to the Eucla Group (redefined by Benbow *et al.*, in press) of the Eucla Basin, and the Plantagenet Group (Cockbain 1968b) of the Bremer Basin. Some of the formations extend laterally from one group to another. Thus, the Princess Royal Spongolite, Pidinga Formation and Hampton Sandstone occur in the Eucla and Eundynie Groups, and the Werillup Formation occurs in both the Plantagenet and Eundynie Groups.

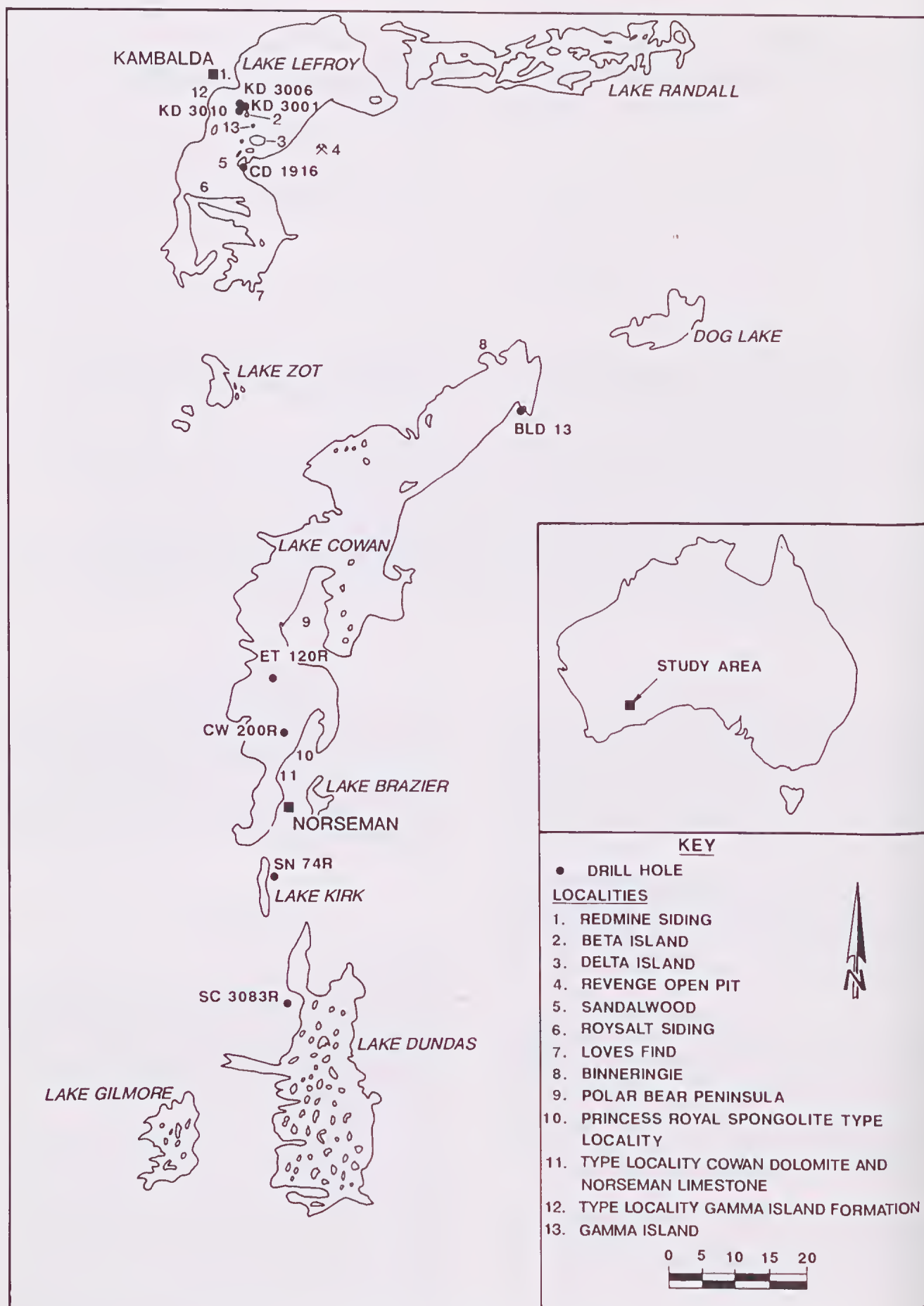


Figure 1. Locality map, showing Lakes Lefroy, Cowan and Dundas.

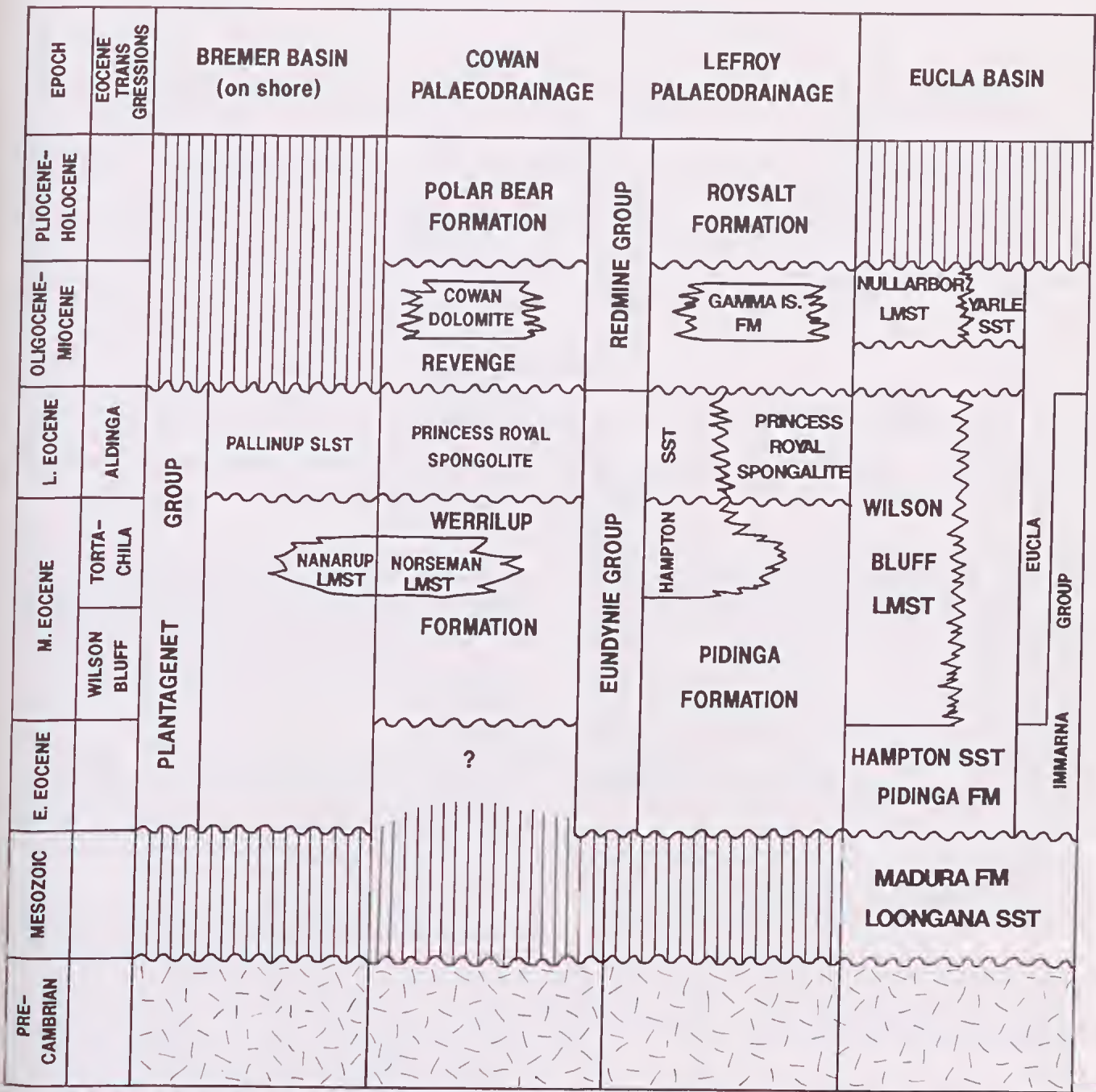


Figure 2. Profile of bedrock beneath Lake Lefroy causeway (from drilling data).

The Eundynie Group has maximum thicknesses of about 100 metres in both the Cowan and Lefroy palaeodrainages, and rests unconformably on Archaean and Proterozoic basement.

The Cowan Dolomite (Fairbridge 1953) was placed in the Eundynie Group by Cockbain (1968a). Drilling by WMC however indicates that the unit occurs within the later Tertiary lacustrine sequence, and is thus part of the overlying Redmine Group.

Pidinga Formation

Numerous names have been proposed for the Eocene sediments in the palaeodrainages of the Yilgarn Craton. Non marine sediments of Eocene age were named the Rollos Bore Beds by Balme and Churchill (1959), after the type locality near Coolgardie. Hocking and Cockbain

(1990) extended the Rollos Bore Formation to include all similar lithologies in palaeodrainages on the Yilgarn Craton. Kern and Commander (in press) reviewed problems with the Rollos Bore locality as a type section, and proposed that the name Wollubar Sandstone, based on work in the Roe and Yindarlgooda palaeodrainages, be used in its place. Similar lithologies are present in the Rebecca and Raeside palaeodrainages to the northeast (Smyth and Button 1989).

The multiplicity of stratigraphic terms for Eocene palaeodrainage sediments along the margins of the western part of the Eucla Basin contrasts with that of the eastern part. In the eastern palaeodrainages, the lignitic marginal marine to non-marine sediments are all placed into the Pidinga Formation, and the non-lignitic, predominantly coarse-grained marginal marine to non-marine sediments Hampton Sandstone (Benbow *et al.* in press). This is practice is continued in this paper.

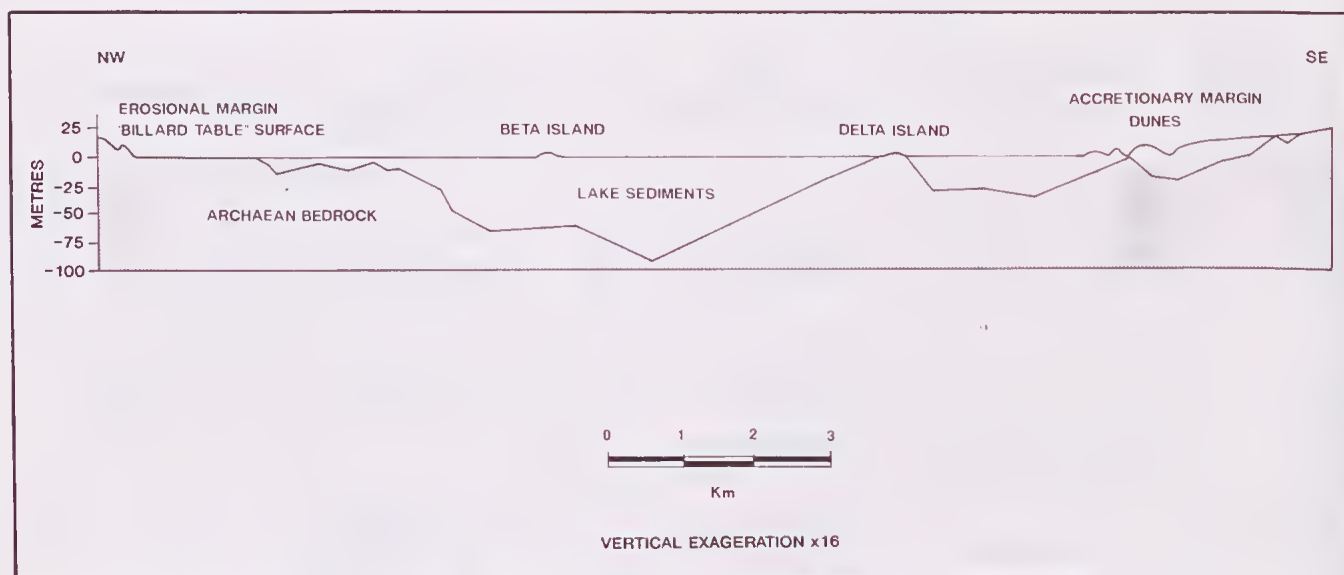


Figure 3. Stratigraphic correlations for the Eucla Platform, palaeodrainage, and Bremer Basin.

In the Lefroy palaeodrainage, the Pidinga Formation consists of laminated red-brown to green silts, white, grey or black clays and silts, and lignite. Gravelly, lignitic sand bodies are locally common. Authigenic pyrite is common throughout the sequence. Organic content varies from very high in lignites to low in white clays. The organic matter occurs as dispersed and comminuted fragments, woody material (most commonly roots, but also stems, seeds, and leaves), and lignite. Rare siliceous spicules are sometimes present. Marine fossils are absent from marginal tributaries such as the Mt Morgan palaeodrainage. Proportions of different lithologies are highly variable. Sedimentary structures, apart from faint laminations, are rare. Thin interbedded gravels are locally present. Scattered quartz granules occur throughout the sequence. A palynomorph assemblage containing 26 species belonging to 12 genera has been recovered from the Pidinga Formation in Lake Lefroy has been described by Parker (1988a, b) and Harris (1989).

The Pidinga Formation rests unconformably on Archaean basement, and interfingers with the Hampton Sandstone. In Lake Lefroy the formation reaches a maximum known thickness of 60 metres in CD 1916.

Palynomorphs described by Parker (1988b) from the Pidinga Formation in Lake Lefroy range in age from Early to Late Eocene. Similar ages were recorded by Balme and Churchill (1959) at Rollos Bore, and by Smyth and Button (1989) from the Rebecca and Raeside palaeorivers.

The Hampton Sandstone interfingers with the Pidinga Formation. The equivalent formation in the Bremer Basin and Cowan Palaeodrainage is the Werillup Formation.

Hampton Sandstone

The Hampton Sandstone is a widespread unit at the base of the Tertiary succession of the Eucla Basin (Lowry 1970). Benbow (1990a) described Hampton Sandstone interfingering with and overlying Wilson Bluff Limestone and spongolites (equivalent to the Princes Royal Spongolite below). Its presence in the Lefroy Palaeoriver to the west of Kambalda was recognised by Jones (1990). The formation is absent from the Cowan palaeoriver.

The Hampton Sandstone consists of fine to gravelly quartz sand. The unit is sparsely to moderately fossiliferous; the most common fossils are siliceous sponge spicules. Opalised gastropods, foraminifera, calcareous sponge spicules, together with brachiopod and echinoderm fragments, are also present. The greatest thickness of Hampton Sandstone yet encountered in Lake Lefroy is 24 metres in KD 3001 (Figure 4).

The Hampton Sandstone overlies and interfingers with the Pidinga Formation and Princess Royal Spongolite. It is most readily differentiated from sands in the Pidinga Formation by the abundance of carbonaceous matter in the latter. Differentiation from the Princess Royal Spongolite is based on the higher sand and lower spicule content of the Hampton Sandstone.

Jones (1990) cited palynological and micropalaeontological data which indicate a Middle to Late Eocene age for the Hampton Sandstone. This age indicates that the formation is pene-contemporaneous with the Pidinga Formation. The lower part of the Hampton Sandstone is correlated with the Tortachila transgression and the upper part with the Aldinga transgression of McGowran (1989). The Pidinga Formation interfingers with the Hampton Sandstone in the eastern and central parts of the Eucla Basin (Benbow *et al.* in press). Sand and sandstones in the Werillup Formation are equivalent to the Hampton Sandstone in the Bremer Basin and Cowan Palaeodrainage.

Werillup Formation

The Werillup Formation (Cockbain 1968b) comprises the basal part of the Plantagenet Group in the Bremer Basin. The formation is widespread along the south coast of Western Australia. The lignitic and carbonaceous sediments of Lake Cowan are correlated with the Werillup Formation because of their similar stratigraphic position, lithology, and depositional environment.

The Werillup Formation consists of carbonaceous clays, silts and sands, together with lignite lenses. A palynological assemblage of 84 species from 57 genera has been recovered from the Werillup Formation at Norseman (Parker 1988b, Harris 1989). The presence of 12 dinoflagellates species belonging to 11 genera was reported by Harris (1989). Siliceous sponge spicules and insect remains are also locally present.

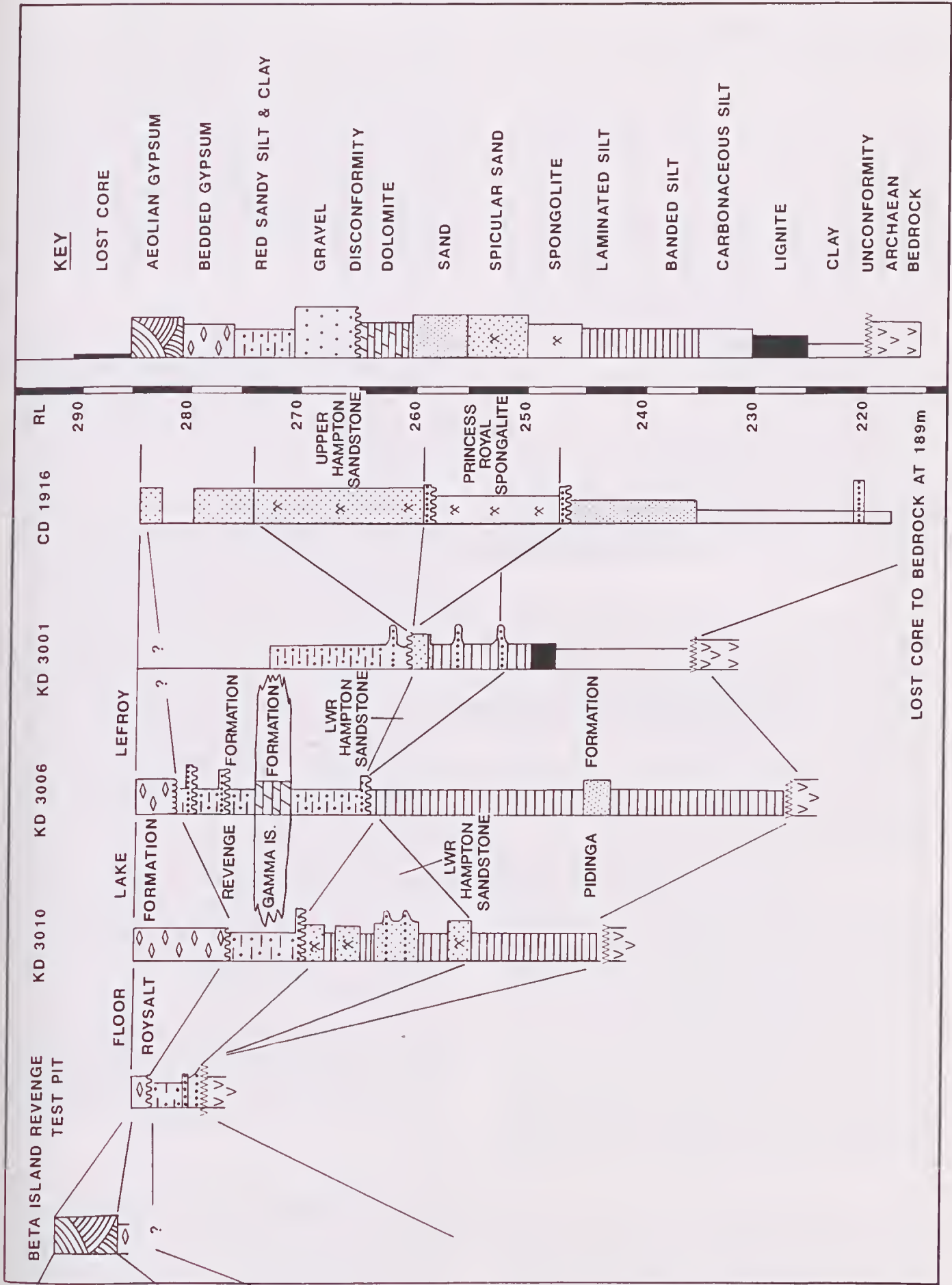


Figure 4. Sub-surface sequence for Lake Lefroy.

Limestones interfingering with the lower part of the Werillup Formation are termed the Nanarup Limestone Member along the south coast and Norseman Limestone in and around Lake Cowan.

The Werillup Formation rests unconformably on Archaean and Proterozoic basement. The formation is disconformably overlain in the palaeodrainages by the Princess Royal Spongolite. Along the south coast it is overlain by the Pallinup Siltstone.

McGowran (1989) demonstrated that the Nanarup Limestone was Middle Eocene. This suggests that clastics underlying the Nanarup Limestone may be Early Eocene, and those overlying late Eocene. Middle Eocene to Late Eocene palynomorphs were described by Parker (1988b) and Harris (1989) from the Werillup Formation from Lakes Cowan and Dundas. The Werillup Formation is equivalent to the Pidinga Formation and Hampton Sandstone of the Lefroy Palaeodrainage and Eucla Basin.

Norseman Limestone

The Norseman Limestone (Gregory 1916) is a fossiliferous marine carbonate that crops out along the south eastern margins of Lake Cowan, and also occurs to the east in Dog Lake (Hooper 1959). Stratigraphic relationships are not evident at the type locality (Clarke *et al.* 1948), but drilling by WMC has revealed that the formation is widespread beneath Lake Cowan (see two drill holes ET120R, CW200R and SN74R in Figure 5).

The Norseman Limestone varies from skeletal wackestone and grainstone to calcareous sandstone. Fossils include bryozoans, gastropods, bivalves, brachiopods, and foraminifera. Cementation varies from complete to non-existent. Rocks at the type locality are silicified, and patchy dolomitisation has occurred in drill hole BLD 13. The formation beneath Lake Cowan, even though largely uncemented, is extensively dolomitised. Trough cross bedding is well developed in outcropping calcarenites near the site of BLD 13 (Figure 6a). Glauconitic material is present in minor amounts, most commonly near the base and top of the formation. The Norseman Limestone reaches a maximum known thickness of 37 metres beneath Lake Cowan in drill hole ET 120R.

Previously unclear stratigraphic relationships have been resolved by drilling in and around Lake Cowan. In BLD 13, the Norseman Limestone gradationally overlies lignitic siltstone of the Werillup Formation and is separated from silicified Princess Royal Spongolite by a thin bed of sandy Werillup Formation. The Werillup Formation overlying the Norseman Limestone towards the middle of Lake Cowan (Figure 5) is, however, up to 30 metres thick.

Foraminiferal data reported by Cockbain (1968a) indicated a Late Eocene age. Palynological studies by Parker (1988b) indicated that the Werillup Formation immediately underlying the Norseman Limestone in BLD 13 is of Early to Middle Eocene age. This indicates that the formation is Middle Eocene or younger. Late Eocene lignitic sediments (Harris 1989) are found overlying the Norseman Limestone.

Cockbain (1968a) correlated the Norseman Limestone with the lithologically similar Toolina Limestone in the Eucla Basin. The Norseman Limestone is however more likely a correlative of the Nanarup Limestone Member of the Werillup Formation in the Bremer Basin. A Middle Eocene age (Tortachila transgression) has been determined

for the Nanarup Limestone Member (McGowran 1989). The southern extension of the Cowan Palaeodrainage into the Bremer Basin at Esperance contains calcareous marine sandstones in the lower Werillup Formation (Cockbain 1967; Morgan & Peers 1973). These are almost certainly equivalent to the Nanarup and Norseman Limestones. This stratigraphic position is contrary to Hocking (1990a), who placed the Nanarup Limestone at the top of the Werillup Formation. The two limestones are thus likely to be the same unit, although more extensive drilling is necessary to confirm this correlation. It is recommended that Nanarup Limestone Member be abandoned as a stratigraphic term, and the earlier name Norseman Limestone Formation be used for all marine carbonates that interfinger with the Werillup Formation.

Princess Royal Spongolite

The Princess Royal Spongolite (Glauert 1926) occurs extensively in palaeodrainages along the eastern margin of the Eucla Basin (Jones 1990). The Formation is common only along the margins of Lefroy and Cowan palaeodrainages, having been removed by erosion from much of the central portions, but is more continuous further east. The Princess Royal Spongolite is absent from tributaries such as the Mt Morgan Palaeodrainage.

Lithologies consisting of greater than 50% siliceous sponge spicules with lesser amounts of silt and clay overlying or interfingering the Pidinga and Werillup Formations are recognised as Princess Royal Spongolite. Minor quartz sand and glauconitic peloids are also present. Other fossils, apart from centric diatoms, are absent. The only description of the spicule assemblage is that of Hinde (1910), who recognised 15 genera at the type locality.

The Princess Royal Spongolite reaches a thickness of 12 metres beneath Lake Lefroy in drill hole CD 1916 (Figure 4). A thickness of 21 metres on the northern shores of Lake Cowan near Bingerie was reported by Hooper (1959).

A disconformable contact marked by a gravel bed separates the Princess Royal Spongolite from the Pidinga Formation in drill hole CD 1916. The Hampton Sandstone interfingers with the Formation at Loves Find, and overlies it in CD 1916. The Princess Royal Spongolite onlaps directly onto Archaean basement along the shores of Lake Lefroy near Loves Find (Figure 6b).

Palynomorphs described by Hos (1977) from Harris Lake on the margins of the Eucla Basin gave a Late Eocene age for the Princess Royal Spongolite. The laterally equivalent Pallinup Siltstone in the Bremer Basin contains a Late Eocene marine fauna (Cockbain 1968b). The Princess Royal Spongolite was probably deposited during the Aldinga Transgression of McGowran (1989).

The formation passes laterally into the Wilson Bluff Limestone to the east (Jones 1990), while the Pallinup Siltstone of the Bremer Basin passes into the Toolina Limestone of the Eucla Basin, east of Israelite Bay (Lowry 1970). The Bring Member of the Pidinga Formation (Bennow 1986) is the time-equivalent lithology in the Tallaringa Palaeodrainage of the eastern Eucla Basin.

Redmine Group

Successions of non-fossiliferous, yellow, brown, and red alluvial and lacustrine sediments were mentioned by Smyth and Button (1989) and Jones (1990). This paper formalises the stratigraphy of the post Eocene succession in Lakes Lefroy and Cowan. The names and their coordinates are taken from localities on the Lefroy 1: 100 000 geological map (sheet 3235), and are shown in Figure 1.

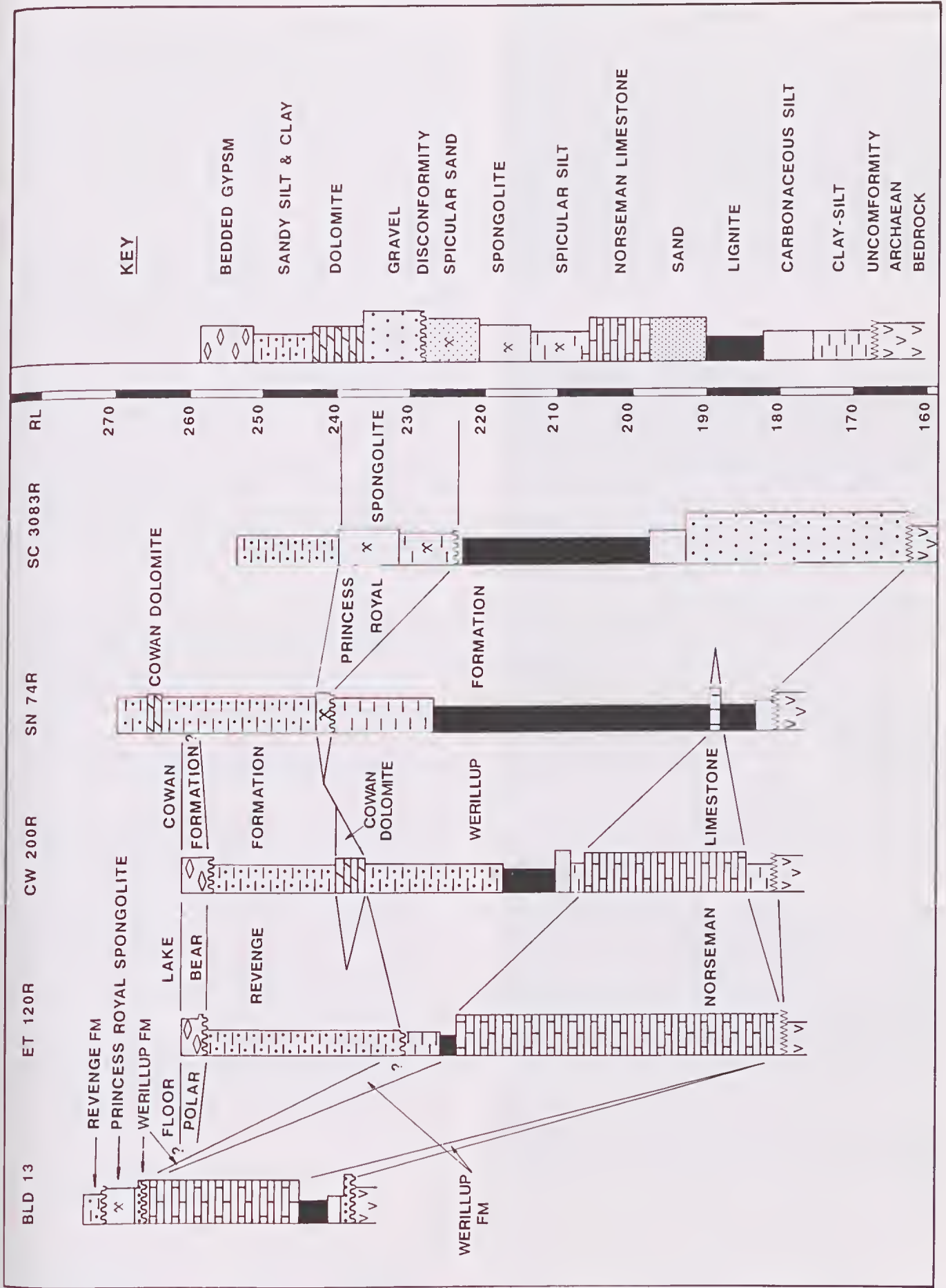


Figure 5. Sub-surface sequence for Lakes Cowan and Dundas.



Figure 6. (A) Outcropping Norseman Limestone on shore of Lake Cowan, near drill hole BLD 13. (B) Outcropping Princess Royal Spongolite and upper Hampton Sandstone on shore of Lake Lefroy, near Loves Find. (C) Outcropping fenestral dolomite of Gamma Island Formation at type locality on Lake Lefroy. (D) Cross-bedded gypsarenite of Beta Island Member, Beta Island.

The Eocene sediments in the Lefroy and Cowan palaeodrainages lack iron oxide bearing sediments; iron oxides and hydroxides are common in the post-Eocene sediments succession. Eocene sediments are fluvial to shallow marine in origin, contrasting with the predominantly lacustrine sediments of the post-Eocene succession. The Eocene palaeodrainage succession can also be correlated with equivalent units on the Eucla Basin, but this cannot be done with the post-Eocene sediments. These differences are sufficient to justify placing the post-Eocene succession into a separate lithostratigraphic unit, the Redmine Group.

The name Redmine Group is taken from Redmine Siding, the railway siding at the Kambalda Nickel Operations concentrator mill (GR 740488). The Redmine Group rests disconformably on the Eocene sediments of Lake Lefroy, up to 20 metres of relief has been incised into the top of the Eundynie Group (Figure 4).

The Redmine Group comprises the post-Eocene portion of palaeodrainage sediments. Red clastic facies occur in Lake Lefroy, further east in the Lefroy Palaeoriver (Jones 1990), and in Lake Cowan. Dark green-grey sediments of presumed post-Eocene age are also present in Lake Cowan. Red-brown sediments in the Raeside and Rebecca palaeodrainages (Smyth & Button 1989) may be equivalent to the Redmine Group. Similar post-Eocene sediments, apart from possible Cowan Dolomite (see below), have not been demonstrated in the Lake Dundas area, but it is highly likely that they are present.

The Redmine Group in the sub-surface consists of predominantly red-brown silts, clays, sand, and gravel. Some sands and gravels are cemented by iron oxides. Dark green clastics are locally present within the group in Lake Cowan. Outcrops are similar, but cemented by iron oxides. Interbedded lenses of oolitic to fenestral dolomite are present. Outcrops of dolomites and iron cemented clastics common along the northern and western margins of Lake Lefroy are also included in the Redmine Group. The upper part of the group contains bedded gypsum deposits and gypsum aeolianites.

Up to 26 metres of predominantly red-brown sediments overlying the Eocene succession are present beneath Lake Lefroy. Similar thicknesses occur beneath Lake Cowan.

The base of the Redmine Group rests disconformably on palaeotopography eroded into Eocene sediments or unconformably on Archaean basement. The variable thickness of the Group is interpreted to be the result of infill of a variably eroded surface. The upper limit of the Redmine Group is the present depositional surface.

The Redmine Group post-dates the late-Late Eocene marine sediments on which it rests, with deposition continuing through to the present. Earliest Pliocene palynomorphs are present in the upper part of the group in Lake Lefroy (Parker 1988a).

The Redmine Group comprises, the Cowan Dolomite together with Revenge, Gamma Island, and Roysalt Formations.

Revenge Formation

The formation is named after Revenge open pit, shown on the Lefroy map sheet at GR 765412, but in reality occurring 500 metres further east at GR 770412.

The Revenge Formation occurs widely beneath Lakes Lefroy and Cowan, and also beneath some of the smaller lakes marginal to them. Similar lithologies occur along the length of the Lefroy palaeodrainage. Lateral continuity between the Lefroy and Cowan palaeodrainages is probable, hence the use of the same stratigraphic name for these lithologies in the two palaeodrainages. The type locality is exposed in the walls of the Revenge open pit, where a thickness of 5 metres is attained.

The Revenge Formation beneath Lakes Cowan and Lefroy consists largely of massive to faintly laminated red-brown silts. Small lenses of fine sand and ferruginous sandstone occur within the formation beneath Lake Lefroy. Red sands and ferruginous sandstones predominate along the margins of the lake. Pebble beds are present at the base of the sequence, and also at intervals higher in the section; these represent internal disconformities. Dark grey-green coloured sediments are locally present. Outcrops of iron oxide cemented conglomerate and sandstone. These well-indurated sediments are marginal facies of the Revenge Formation. The Revenge Formation in Lake Cowan is composed of similar lithologies to those found in Lake Lefroy (Figure 5).

The formation reaches a known thickness of 17 metres in Lake Lefroy. Marginal facies of the Revenge Formation exposed on the shores of Lake Lefroy occur at elevations 8 metres above the present lake surface, indicating original thicknesses at least 8 metres greater than that presently preserved. The formation may reach thicknesses of 25 metres in Lake Cowan (Figure 5).

The base of the formation rests unconformably on Archaean bedrock, as displayed in the Revenge open pit, or disconformably on Eocene sediments. The upper limit of the unit is the disconformable base of the overlying Roysalt Formation in Lake Lefroy and the Polar Bear Formation in Lake Cowan.

The oxidised nature of the Revenge Formation is not favourable for the preservation of palynomorphs, and none have been recovered. A lower limit for the formation is set by the underlying Late Eocene sediments, and the overlying Pliocene pollen assemblage in the Roysalt Formation (Parker 1988a). A Miocene age is favoured, given the widespread preservation of lacustrine sediments from this time elsewhere in Australia (De Deckker 1988). This also coincides with the last major transgression on the Eucla Basin that deposited the Nullarbor Limestone (Lowry 1970), the elevated base level resulting in lacustrine deposition within marginal palaeodrainages.

The Perkollilli Shale (Kern & Commander, in press) in the Roe Palaeodrainage is lithologically very similar, and is probably correlative with the Revenge Formation. The Miocene fluvial to marginal marine Plumbridge Formation (Hocking 1990b) and the marine Yarle Sandstone (Benbow 1990b) along the margins of the Eucla Basin are likely to be distal equivalents. Some of the numerous Cainozoic formations defined by Glassford (1987) from Yeelirie may be partly equivalent to the Revenge Formation.

Gamma Island Formation

The Gamma Island formation is named after Gamma Island, the local name for the Lake Lefroy island shown at GR 775539 on the Lefroy map sheet. The formation occurs patchily beneath Lake Lefroy, and along its northern and western margins. The shore of Lake Lefroy at the Newtown Creek estuary (Figure 1, 6c).

Lenses of oolitic (L. Killigrew, quoted by Loftus-Hills 1981) and fenestral dolomite are present in drill hole KD 3006 (Figure 4). White oncolitic, fenestral, peloidal, and massive dolomites to dolomitic carbonate mudstones are present on the margins and estuaries of Newtown, Merougil and Muldolia Creeks (Figure 1).

The thickness varies from at least 2 metres in the type locality, to 2.5 metres in KD 3006.

Boundary relationships are not exposed at the type locality. The Gamma Island Formation occurs within the Revenge Formation in KD 3006, and overlies it along the western shores of Lake Lefroy.

A Miocene age is favoured, given the widespread preservation of lacustrine sediments, especially carbonates, from this time elsewhere in Australia (De Deckker 1988).

The Gamma Island Formation is placed in a separate formation from other units in the Redmine Group because its marked lithological contrast to them, and for consistency of usage with equivalent units, the Cowan Dolomite in Lake Cowan, and the Garford Formation is the palaeodrainages of the eastern Eucla Basin (Benbow *et al.* in press). The lack of continuity between the otherwise similar lacustrine carbonates of Lakes Lefroy and Cowan justifies the use of different formation names.

Cowan Dolomite Formation

The relationship of the Cowan Dolomite (Fairbridge 1953) to the Norseman Limestone and Princess Royal Spongolite is not evident at the type locality, although the three units are spatially closely associated. Aircore drilling at Lake Kirk south of Norseman has revealed similar lithologies occurring at different levels with lacustrine sediments overlying the Princess Royal Spongolite. The formation is thus placed within the Redmine Group.

The Cowan Dolomite crops out along the shores of Lakes Cowan and Brazier. The formation consists of white to buff-coloured dolomite to dolomitic carbonate mudstone. The maximum thickness of the Cowan Dolomite is unknown, in SN 78R it is 2 metres thick. The Cowan Dolomite is equivalent to the Gamma Island Formation in Lake Lefroy. Small outcrops of dolomite in the Cowan palaeodrainage east of Salmon Gums (to the south of Lake Dundas) were correlated with the Cowan Dolomite by Doepel (1973).

The age of the formation is unknown, but is probably Miocene. Carbonate facies are common in Miocene lacustrine sediments elsewhere in Australia (De Deckker 1988), the Formation may be partly equivalent to the Miocene-Pliocene Garford Formation in palaeodrainages of the eastern Eucla Basin (Benbow *et al.* in press).

Roysalt Formation

The name Roysalt Formation is derived after Roysalt Siding, GR 688271, near the old Lake Lefroy salt works. The unit occurs right across the floor of Lake Lefroy and on its margins. Type exposures of the formation occur in the walls of the Revenge open pit, where thicknesses of 1.5-2m are attained.

The Roysalt Formation consists of sandy silts and clays on the margins of Lake Lefroy, passing into bedded gypsum crystals in a silty, carbonaceous, and pyritic matrix towards the centre of the lake. Gypsum crystals in the lower part of the formation have grown together to form a boxwork structure. The sediments in the gypsum dunes have been separated into the Beta Island Member (see below).

The greatest known thickness is 9 metres (KD 3010, Figure 4). Horizontally bedded gypsum occurs up to 1 metres above the present lake floor in gypsum dune islands, where overlying gypsum aeolianite has protected the sediments from erosion.

The Roysalt Formation rests disconformably on the erosional top of the Revenge Formation. Preservation of similar sediments above the current lake floor in gypsum dune islands indicates a minimum thickness of 1 metres for eroded material, which demonstrates that the current lake floor is an erosional surface.

Palynomorphs from the base of the formation at Revenge give a Pliocene age (Parker 1988a). Deposition of the Roysalt Formation may have continued into the Holocene.

The Roysalt Formation is a time equivalent of Pliocene sediments at Lake Tay, west of Lake Dundas (Bint 1981), the Darlot Formation (in particular the Miranda Member) at Yeelirie (Glassford 1987), and of the Pliocene Narlaby Formations (Benbow *et al.* in press) in South Australia. The formation passes laterally into, and interfingers with fluvial and aeolian clastic sediments along the margins of Lake Lefroy. The Polar Bear Formation is the equivalent unit in Lake Cowan (see below). Different formation names are used owing to the lack of continuity between the different evaporitic lithologies of Lakes Cowan and Lefroy.

Beta Island Member

The name Beta Island Member is taken from Beta Island, the local name for the gypsum dune island at GR 765412, site of the Lake Lefroy land sailing club.

The Beta Island Member comprises the gypsum dunes that occur across the lake floor and on its western margins. Most islands on Lake Lefroy are at least in part gypsum dunes. Some, such as Delta Island, are composite, with a bedrock core and accreted gypsum and silica dunes. The member also occurs along the lake shore, particularly at Sandalwood. The 8 metres high cliffs that surround most of the margin of Beta Island (Figure 6d) comprise the type locality for the Member.

The Beta Island Member is composed of gypsum cemented, steeply cross-bedded, gypsum sand. Quartz sand, silt and clay are minor components. Individual cross bed sets range in thickness from 4-8 metres. Two gypcrete horizons are present within the member on Beta Island. The uppermost horizon corresponds with the present surface in each case.

The member reaches a maximum thickness of 11 metres on Oyster Island.

The Beta Island Member overlies the Roysalt Formation. The contact is exposed approximately 1 metre above the lake floor on Beta Island where cross bed toes transgress across flat bedded gypsum. The present land surface corresponds with the top of the member.

The age of the Beta Island Member is unknown. The gypsum dunes must post date the Pliocene and younger Roysalt Formation from which it is derived. The member is currently being eroded, with cliff faces developed on nearly all exposures. Mixed quartz-clay dunes have also partly buried gypsum dunes on Delta Island and at Sandalwood; the member is thus unlikely to be Holocene in age. Bowler (1976) dated many gypsum dunes in arid Australia at 13-18 000 years BP, a possible age for the Beta Island Member.

The Beta Island Member is closely associated with siliciclastic dune sediments, both on the lake islands and shores. The gypsum dunes underlie siliciclastic dunes in many localities, the stratigraphic relationship between the Beta Island Member and older, degraded dune systems is unclear. The member is equivalent to part of the Miranda Member of the Darlot Formation at Yeelirie (Glassford 1987).

Polar Bear Formation

The Polar Bear Formation is named after Polar Bear Peninsula, the large peninsula extending out into Lake Cowan north of Norseman. The Polar Bear Peninsula occurs on the Cowan topographic sheet at GR 870680. The Polar Bear Formation occurs across the floor of Lake Cowan and on its margins. The type section is in CNG air core hole ET 120R, where the formation is 3 metres thick.

The Polar Bear Formation consists of sandy silts and clays along the edges of Lake Cowan, and bedded gypsum crystals in a silty matrix towards the centre of the lake. Low relief gypsum dunes occur in some localities along the floor of Lake Cowan and its margins. These dunes are generally less than 2 metres high.

The Formation is 3 metres thick in ET 120R and CW 200R (Figure 5). Scattered low relief gypsum dunes along the margins of the lake and across its floor add another 2 m.

The Polar Bear Formation rests disconformably on the erosional top of the Revenge Formation. The top of the formation is defined by the present land surface.

The Formation is earliest Pliocene to Holocene in age, by analogy with the lithologically and stratigraphically equivalent Roysalt Formation in Lake Lefroy. Early Pliocene pollen in sediments in Lake Tay 125 kilometres to the south-west (Bint 1981) indicate the presence of non-arid lake shore vegetation. This indicates that gypsum precipitation in Lake Tay began after the Early Pliocene. Thus the base of the Polar Bear Formation in Lake Cowan (about half way between Lakes Lefroy and Tay), may be slightly younger than earliest Pliocene.

Conclusions

This proposed stratigraphic framework is intended to simplify and clarify the stratigraphy of the Cowan and Lefroy palaeodrainages, and relate them to the stratigraphy of the Bremer and Eucla Basins. It is hoped that the same stratigraphic nomenclature, with appropriate modifications for local units (particularly in the Redmine Group) can be extended to other palaeodrainages along the margins of the Bremer and Eucla Basins.

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References

- Balme B E & Churchill D M 1959 Tertiary sediments at Coolgardie, Western Australia. *Journal of the Royal Society of Western Australia* 42: 37-43.
- Benbow M C 1986 Tallaringa map sheet. Geological Atlas of South Australia, 1: 250 000 series. South Australian Department of Mines and Energy, Adelaide.
- Benbow M C 1990a Tertiary Coastal Dunes of the Eucla Platform, Australia. *Geomorphology* 3: 9-29.
- Benbow 1990b The Yarle Sandstone: a Miocene coastal terrigenous sequence of the Eucla Platform. *Quarterly Geological Notes of the Geological Survey of South Australia* 113: 2-6.
- Benbow M C, Lindsay J M & Alley N F in press Bight and Duntroon basins, Eucla Basin and palaeodrainage. In: *The Geology of South Australia* (ed Johns R K) Geological Survey of South Australia Bulletin, South Australian Department of Mines and Energy, Adelaide.
- Bint A N 1981 An Early Pliocene pollen assemblage from Lake Tay, South-western Australia, and its phytogeographic implications. *Australian Journal of Botany* 29: 277-91.
- Bowler J M 1976 Aridity in Australia: Age, Origins and Expression in Aeolian Landforms and Sediments. *Earth Science Reviews* 12: 279-310.
- Bunting J A, Van de Graaff W J E, & Jackson M J 1974 Palaeogeography of the Eastern Goldfields, Gibson Desert and Great Victoria Desert. *Geological Survey of Western Australia Annual Report* 1973: 45-50.
- Campbell W D 1906 The geology and mineral resources of the Norseman district, Dundas Goldfield. *Western Australian Geological Survey Bulletin* 21. Geological Survey of Western Australia, Perth.
- Clarke E De C, Teichert C & McWhae J R H 1948 Tertiary deposits near Norseman, Western Australia. *Journal of the Royal Society of Western Australia* 32: 85-103.
- Clarke J D A In press Evolution of the Lefroy and Cowan palaeodrainages, Western Australia. *Australian Journal of Earth Sciences*.
- Cockbain A E 1967 *Asterocyclina* from the Plantagenet Beds near Esperance, WA. *Australian Journal of Science* 30: 68-69.
- Cockbain A E 1968a Eocene foraminifera from the Norseman Limestone of Lake Cowan, Western Australia. *Geological Survey of Western Australia Annual Report* 1967, 59-60.
- Cockbain A E 1968b The stratigraphy of the Plantagenet Group, Western Australia. *Geological Survey of Western Australia Annual Report* 1967, 99-101.
- De Deckker P 1988 Large Australian lakes during the last 20 million years: sites for petroleum source rock or metal ore deposition, or both? In: *Lacustrine Petroleum Source Rocks* (eds Fleet A J, Kelts K, & Talbot M R) Geological Society Special Publication, London 40: 45-58.
- Doepel J J G 1973 Explanatory notes on the Norseman 1: 250 000 geological sheet, Western Australia. Geological Survey of Western Australia, Perth.
- Fairbridge R W 1953 *Australian Stratigraphy*. University of Western Australia Text Books Board, Perth.
- Gibson C G 1909 The geological features of the country lying along the route of the proposed transcontinental railway in Western Australia. *Geological Survey of Western Australia Bulletin* 37.
- Glassford D K 1987 Cainozoic stratigraphy of the Yeelirie area, northeastern Yilgarn Block, Western Australia. *Journal of the Royal Society of Western Australia* 70: 1-24.
- Glauert L 1926 A list of Western Australian fossils, supplement No. 1: Western Australian Geological Survey Bulletin 88: 36-71.
- Gregory J W 1916 The age of the Norseman Limestone, Western Australia. *Geological Magazine* 3: 320-321.
- Griffin T J 1989 Explanatory notes on the Widgiemooltha 1: 250 000 geological sheet, Western Australia. Geological Survey of Western Australia Record 1989/4.
- Harris W K 1989 Palynology of seven samples from the Norseman area. Unpublished report, Kambalda Nickel Operations Geological Exploration File 9/G/6L.
- Hinde G J 1910 On fossil sponge spicules in a rock from the Deep Lead (?) at Princess Royal Township, Norseman District, Western Australia. *Geological Survey of Western Australia Bulletin* 36: 7-24.
- Hocking R M 1990a Bremer Basin. In: *Geology and Mineral Resources of Western Australia: Geological Survey of Western Australia Memoir*, Perth 3: 561-563.
- Hocking R M 1990b Eucla Basin. In: *Geology and Mineral Resources of Western Australia: Geological Survey of Western Australia Memoir*, Perth 3: 548-561.
- Hocking R M & Cockbain A E 1990 Regolith. In: *Geology and Mineral Resources of Western Australia*. Department of Mines Western Australia Memoir, Perth 3: 591-601.
- Hooper K 1959 The marine Tertiary rocks of Bingeri at the north end of Lake Cowan, Western Australia. Carlton University Department of Geology Paper, Ottawa 59-3.
- Hos D P C 1977 Samples from Harris Lake, Western Australia. University of Western Australia Palynology Report 351.
- Jones B G 1990 Cretaceous & Tertiary sedimentation on the western margin of the Eucla Basin. *Australian Journal of Earth Sciences* 37: 317-329.
- Kern A M & Commander P 1993 Cainozoic stratigraphy in the Roe Palaeodrainage of the Kalgoorlie region, Western Australia. Geological Survey of Western Australia, Perth. Professional Paper 34.
- Loftus-Hills G 1981 Contingency report on the palynological work on the Lake Lefroy area by Dirk Hos. Kambalda Nickel Operations Geology Department unpublished technical report 1304.
- Lowry D C 1970 Geology of the Western Australian part of the Eucla Basin. Geological Survey of Western Australia Bulletin 122. Geological Survey of Western Australia, Perth.
- McGowran B 1989 The later Eocene transgressions in southern Australia. *Alcheringa* 13: 45-68.
- Morgan K H & Peers R 1973 Explanatory notes on the Esperance-Modrain Island 1: 2500 000 geological sheet, Western Australia. Geological Survey of Western Australia, Perth.
- Parker F 1988a Palynology of Samples from Lake Lefroy. Kambalda Nickel Operations Geology Department unpublished technical report 2922.
- Parker F 1988b Palynology of selected drill hole samples from the Lake Lefroy area. Kambalda Nickel Operations Geology Department unpublished technical report 3000.
- Smyth P R & Button A 1989 Gold Exploration in the Tertiary Palaeodrainage Systems of Western Australia. In: *World Gold '89* (eds Bhappu R B & Harton R J). Gold forum on technology and practices. Proceedings of the First Joint International Meeting between the Society of Mining Engineers and the Australasian Institute of Mining and Metallurgy, Reno Nevada, p262-269. Society of Mining, Metallurgy and Exploration, Littleton, Colorado.
- Van de Graaff W J E, Crowe R J, Bunting J A & Jackson M J 1977 Relict Early Cainozoic Drainage in arid Western Australia. *Zeitschrift fur Geomorphologie N.F.* 21: 379-400.
- Woodward N P 1897 The Dry Lakes of Western Australia. *Geological Magazine* 4: 363-366.

Aquatic invertebrate fauna of the Two Peoples Bay area, southwestern Australia

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Abstract

The aquatic invertebrate fauna of four rivers and streams and three lakes in the Two Peoples Bay area, southwestern Australia, was sampled in June 1990 and February 1991. A total of 247 taxa were recorded: 110 in flowing waters, 170 in standing waters and 33 common to both habitats. Increased sampling intensity in February 1991 revealed a diverse microinvertebrate fauna of 47 taxa of Protozoa and Rotifera.

The macroinvertebrate fauna was similar to that reported previously from aquatic ecosystems in southwestern Australia. Thirty-six species of microinvertebrates (2 Protozoa, 21 Rotifera, 10 Cladocera and 3 Copepoda) were new records for southwestern Australia and, in many cases, Australia. The number of new records reflects greater sampling and taxonomic effort than has been used previously in southwestern Australia, but also suggests southwestern Australia may have a distinctive microfauna.

Introduction

Two Peoples Bay is an important area for wildlife conservation. It is best known as the last refuge for the Noisy Scrub-bird *Atrichornis clamosus* and a nature reserve was proclaimed in 1966 to protect this species. Because of the significance of the reserve there have been numerous surveys of its terrestrial flora and fauna, as well as detailed studies of the Noisy Scrub-bird (Smith 1985, Smith & Calver 1984).

Wetlands form a significant component of the reserve, comprising between 8.5% and 15.8% of the 4745 ha depending on time of year. The reserve and adjacent area contain three major lakes, two small rivers and numerous creeks. Water depth, salinity and pH of the lakes have been monitored for a number of years (Lane & Munro 1983) and their waterbird populations have been surveyed (Jaensch *et al.* 1988, Halse *et al.* 1992).

This paper reports results of surveys of the aquatic invertebrate fauna of the Two Peoples Bay area in June 1990 and February 1991. Results are compared with data from aquatic invertebrate work elsewhere in southwestern Australia. For streams these data come principally from the northern jarrah forest and Swan Coastal Plain (Bunn *et al.* 1986, Storey & Edward 1989, Storey *et al.* 1990), the karri forest (Growth & Davis 1991, Growth 1992) and the southern acid peat flats (Pusey & Edward 1990).

Studies of fresh lentic waterbodies have been restricted to permanent and seasonal wetlands on the Swan Coastal Plain (Balla 1993, Davis *et al.* 1993, Growth *et al.* 1992) and the southern acid peat flats (Pusey & Edward 1990), temporary pools on granite outcrops south of 32° latitude (Bayly 1982), and wetlands of the Lake Muir system (DeHaan 1987).

Study area

Two Peoples Bay (34°57'S 118°10'E) is located on the south coast of Western Australia, approximately 25 km east of Albany. The area contains three distinct drainage systems: the Goodga, the Angove, and the upland streams of the Mt Gardner headland (Fig 1).

The Goodga system comprises the Goodga River, Moates Lake and Gardner Lake and enters the sea in Two Peoples Bay. The slow-flowing Goodga River arises approximately 20 km inland. In its upper reaches, the river flows through cleared farmland before entering the reserve and discharging into Moates Lake (Fig 1).

Moates Lake has an area of 144 ha, 82 ha of which consists of fringing sedges. It is one of the deepest natural lakes in southwestern Australia, with a maximum depth of c. 5 m. Much of the southern shore has been inundated by a large calcareous sand dune. The Goodga River flows from Moates Lake into Gardner Lake, which covers 164 ha and has 25 ha of fringing sedges and occasionally inundated woodland. There is occasional inflow from the sea into Gardner Lake during spring tides and storm surges.

The Angove system consists of the Angove River and Angove Lake and joins the Goodga system on the seaward side of Gardner Lake. The Angove River is short (14 km) and moderately fast-flowing. The upper reaches of the river flow through uncleared Water Reserve but there is some cleared farmland around the lower reaches (Fig 1). The river is regulated by a pipehead dam built in 1912-13 to supply water to the town of Albany. Situated downstream of the dam, Angove Lake has an area of 50 ha. It contains very extensive beds of sedges and little open water; associated swamps and inundated land around the lake increase the overall wetland area to 120 ha.

The streams of the Mt Gardner headland system flow through dense shrub/heath in steep incised gullies. Websters Gully and West Gully are permanent and flow into the sea, some of the streams flow inland to disappear at the base of the headland.

Methods

Study sites were selected on the three lakes, on the main channels of the two rivers and on the lower reaches of West and Websters Gullies, which were chosen as being representative of permanent streams on Mt Gardner headland (Fig 1).

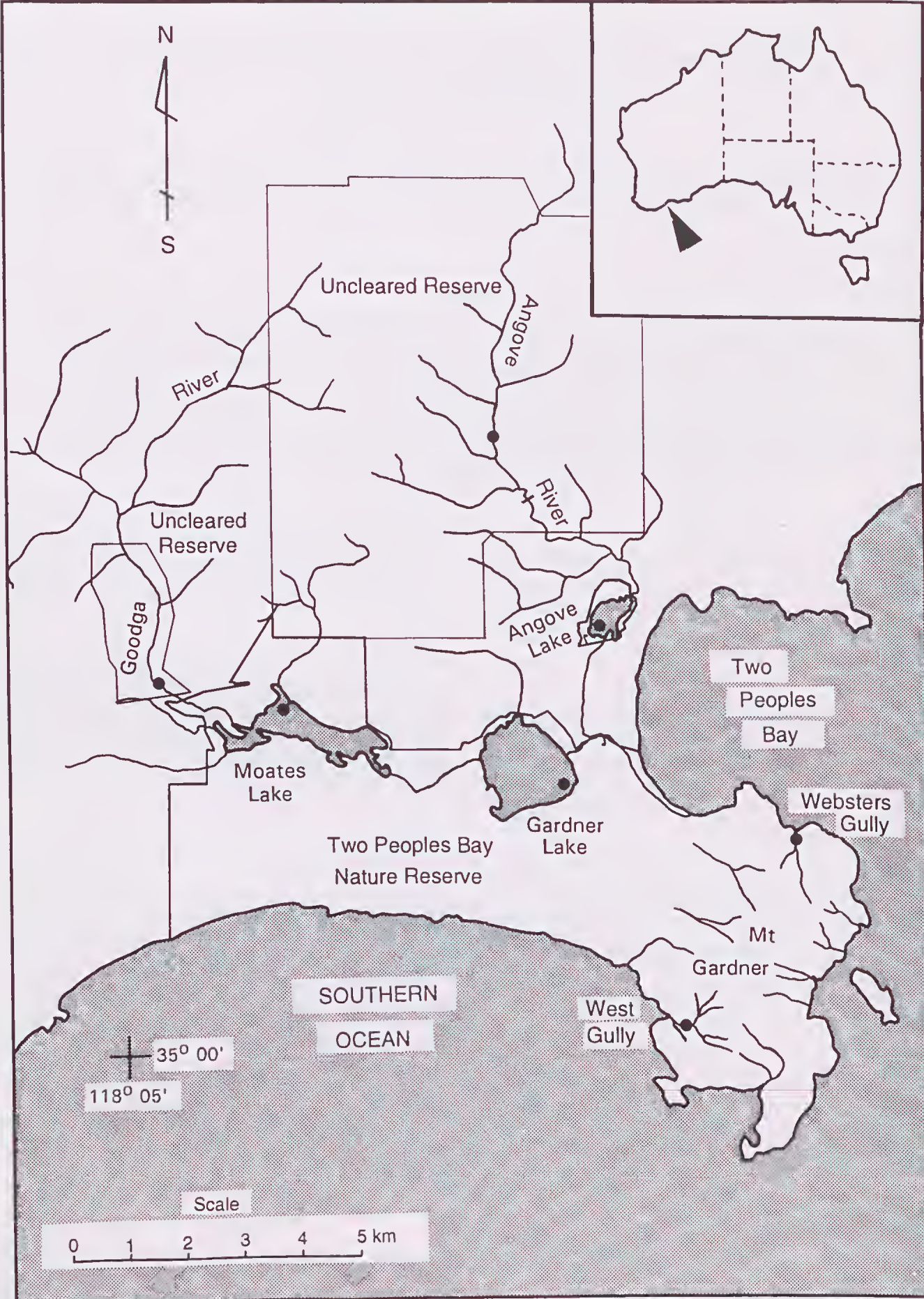


Figure 1. Streams and lakes, showing the location of the sampling sites in the Two Peoples Bay area. There is a small part of Two Peoples Bay Nature Reserve around Angove Lake

Qualitative samples of the aquatic invertebrate fauna at each site were collected in June 1990 and February 1991. Additional samples of Cladocera were taken in September 1990. All major habitats (*i.e.* water column, submerged and emergent macrophytes, leaf litter, submerged wood, organic deposits, sand/gravel beds, cobbles and bedrock) were sampled by hand and with standard FBA pondnets in June and February to maximise the number of taxa collected. Rivers and streams were sampled using a mesh size of 250 µm. Lakes were sampled initially with a mesh size of 110 µm but this was reduced to 50 µm in September and February to retain more microinvertebrates.

In the laboratory, samples were elutriated in water to separate organic and inorganic fractions. Invertebrates were removed from organic fractions by eye and under a binocular dissecting microscope. Specimens were usually identified to genus or species. When this was not possible, specimens were matched with previously curated voucher specimens. Apparently new microinvertebrate taxa were stored in 10% glycerol/water on microslides for later taxonomic treatment.

In association with the invertebrate sampling, water depth, salinity (total dissolved solids; TDS), pH, temperature and dissolved oxygen (expressed as percentage saturation) were measured at each site on each occasion.

Community composition in lotic and lentic sites at Two Peoples Bay was compared, on the basis of major taxonomic groups, with previous studies in similar habitats in southwestern Australia.

Results

Salinity was <1 g L⁻¹ TDS in all waterbodies except Gardner Lake in both winter and summer (Table 1). There was little seasonal variation in salinity of Angove River, Goodga River or Moates Lake but it increased three-fold in Gardner Lake in summer to 2.55 g L⁻¹ TDS.

Most of the water-bodies were neutral with respect to pH but Angove River was slightly acidic and Gardner Lake was alkaline in summer (Table 1). Angove River, West Gully and Websters Gully had the lowest water temperatures in summer, which reflected a greater amount of shading. Where sampled, the Goodga River was an open channel with little riparian vegetation. Dissolved oxygen levels were high in winter at all sampling sites except Angove River and in flooded woodland at Gardner Lake.

In summer, dissolved oxygen levels were very low in West Gully and Websters Gully and moderately low in Angove River (Table 1). West Gully had stopped flowing when sampled in summer and consisted of a series of shallow pools; flow rate was very low in Websters Gully. Angove River continued to flow moderately strongly in summer but the flow rate was low in Goodga River, which had become virtually a series of long pools.

A total of 247 taxa of invertebrates were collected from the seven sites (see Appendix). Excluding protozoans and rotifers (because sampling effort was unequal between seasons), 127 taxa were collected in winter, 152 in summer and 79 taxa were common to both seasons. Thirty-nine per cent and 45 per cent of taxa were restricted to flowing and standing waters, respectively. Seventy-five per cent of the 33 taxa common to both flowing and standing waters were present in both seasons. Of the taxa restricted to one type of water-body, 32 per cent were present in both seasons.

Rivers and streams contained 110 taxa (see Appendix). Sixty-three taxa were collected in winter and 96 in summer, with 45 per cent of the fauna being common to both seasons. Eighty-three taxa were collected from the two 'lowland' rivers and 56 from the headland streams, with 11 per cent of the fauna being common to the four sites. Angove River contained 53 taxa, with 55, 40 and 43 taxa taken from Goodga River, West Gully and Websters Gully, respectively.

The three lakes contained 170 taxa (see Appendix). Excluding protozoans and rotifers, 95 taxa were taken in winter, 93 in summer and 30 per cent of the fauna was common to both seasons. Including protozoans and rotifers, 96 taxa occurred in Angove Lake, 72 in Gardner Lake, 85 in Moates Lake. Seventeen per cent of the fauna was common to the three lakes.

The rivers and streams were dominated by insects whereas the lakes were dominated by crustaceans and rotifers (see Appendix).

Discussion

Community composition

Few species (17%) occurred in all three lakes at Two Peoples Bay. The same phenomenon was noted in closely adjacent billabongs on the River Murray floodplain by Hillman & Shiel (1991). They proposed that species were responding to inter-habitat differences and that different species occurred under slightly different conditions.

Table 1
Some physical and chemical parameters of the streams and lakes at Two Peoples Bay that were sampled for invertebrates in June 1990 (Winter) and February 1991 (Summer).

Parameter	Season	Angove River	Goodga River	West Gully	Websters Gully	Angove Lake	Gardner Lake	Moates Lake
Depth (m)	W	0.50	0.40	0.40	0.30	1.75	2.60	4.39
	S	0.40	0.30	0.20	0.60	1.59	1.82	3.96
Salinity (g L ⁻¹)	W	0.25	0.56	0.44	0.18	0.58	0.88	0.47
	S	0.26	0.52	0.55	0.32	0.64	2.55	0.42
pH	W	5.88	6.31	6.54	6.75	6.78	7.60	6.68
	S	5.65	6.29	6.00	6.66	7.13	8.98	7.27
Temp (°C)	W	13.1	11.4	10.8	11.4	13.3	10.7	11.5
	S	16.6	23.7	16.8	16.2	26.0	22.6	25.5
D.O. (%)	W	72.0	87.0	93.0	93.0	96.0	99.5*	95.5
	S	67.0	91.0	29.0	49.0	114	117	116

*23% in flooded melaleuca woodland

Overall, the rivers and streams at Two Peoples Bay were similar in community composition to other streams studied in southwestern Australia (Table 2). The number of taxa varied considerably between studies but that may have been a result of different numbers of sampling sites and sampling frequency.

In contrast, community composition appeared to vary among the lake studies (Table 2), with Two Peoples Bay being dominated by microinvertebrates while the peat lakes, especially, contained relatively more insects. Without additional sampling, it is unclear how many of the differences between lakes were a result of different sampling methods, sampling intensity and varying taxonomic effort. It should be noted, however, that rotifers were examined only in the Two Peoples Bay study and, owing to the nature of the project, little effort was spent identifying microcrustaceans or chironomids at Lake Muir (DeHaan 1987).

Seasonality

Seasonality was evident in the occurrence of some taxa from both flowing and standing waterbodies at Two Peoples Bay. For example, the chironomids *Cladopelma curtivalva*, *Procladius paludicola*, ?*Harnischia* sp. VTPB4,

Cladotanytarsus ?mancus, *Chironomus* aff. *alternans*, the empidid larva, the trichopteran *Helyethira malleoforma* and the copepod *Eucyclops australiensis* were recorded only in summer (see Appendix).

The chironomids *Orthocladinae* sp. VTPB1, *Tanytarsini* sp. A, *Orthocladinae* sp. A, the coleopteran *Lancetes lanceolatus*, the cladoceran cf. *Pleuroxus* sp. A, the copepods *Microcyclops* sp. A and *Onychocamptus chathamensis* were collected only in winter.

Seasonality of aquatic invertebrates in streams of the northern jarrah forest has been reported previously (Bunn *et al.* 1986, Storey *et al.* 1990). Bunn *et al.* (1986) proposed that the predictable climate of southwestern Australia resulted in the aquatic fauna of forested streams developing synchronized life-cycles (Bunn 1988) that give rise to distinct differences between the faunas of winter and summer. Seasonality has also been observed in the aquatic fauna of streams in the karri forest (Grown & Davis 1991, Grown 1992). It is likely that this pattern applies to most waterbodies of southwestern Australia but, with the exception of Balla (1993), there are no data on life histories and seasonality of invertebrates in standing waters.

Table 2

Number of taxa identified in major taxonomic groupings in studies of the invertebrate fauna of some rivers, streams and lakes in south-western Australia

	Streams				Lakes			
	Two Peoples Bay ¹	Jarrah forest ²	Karri forest ³	Acid peat flats ⁴	Two Peoples Bay ¹	Swan Coastal Plain ⁵	Peat lakes ⁶	Acid peat flats ⁴
Protozoa	—	—	—	—	6	—	—	—
Rotifera	—	—	—	—	41	—	—	—
Nematoda	1	1	1	—	1	1	—	—
Mollusca	1	8	3	1	2	13	5	2
Annelida	1	1	1	1	1	5	3	1
Arthropoda								
Arachnida	8	1	10	4	6	20	11	9
Crustacea								
Cladocera	1	5	—	4	26	37	1	5 ⁷
Ostracoda	3	5	3	4	9	26	5	8 ⁷
Copepoda	4	9	—	4	17	10	1	4 ⁷
Decapoda	4	3	1	1	4	2	3	1
Amphipoda	5	4	4	3	2	3	2	3
Isopoda	3	2	1	2	2	1	1	1
Others	—	—	—	—	—	1	—	—
Insecta								
Diptera								
Chironomidae	28	86	36	27	24	23	9	30
Others	15	44	56	13	10	20	5	8
Odonata	8	17	7	—	3	13	5	1
Hemiptera	—	10	2	—	3	18	12	2
Ephemeroptera	4	7	9	2	1	2	1	2
Plecoptera	2	3	2	1	—	—	—	2
Trichoptera	13	36	20	9	5	5	10	13
Coleoptera	7	33	11	4	7	42	23	11
Others	2	1	2	—	—	1	2	—
Others	—	11	2	—	—	2	—	—
TOTAL	110	287	171	80	170	245	99	103
NO. OF SITES	4	>30	22	2	3	40	4	6 ⁷
NO. OF SAMPLING OCCASIONS	2	12	12 ⁸	5	2	3	2	5 ⁷

¹This study

²Bunn *et al.* (1986), Storey & Edward (1989), Storey *et al.* (1990)

³Grown & Davis (1991), Grown (1992)

⁴Pusey & Edward (1990)—Collembola omitted

⁵Davis *et al.* (1993), Grown *et al.* (1992)

⁶De Haan (1987)—Collembola omitted

⁷Extra sampling by I A E Bayly

⁸Ten sites were sampled only four times

Some life history strategies result in taxa being present in waterbodies all year. For example, the amphipod *Uroctena setosa*, the trichopteran *Smicrophylax australis* and the anisopteran *Austroaeschna anacantha* are known to require more than one year to reach maturity (Bunn 1988) and, therefore, it is not surprising that they occurred in both summer and winter at Two Peoples Bay. The ephemeropteran *Nyungara bunnii* and the trichopteran *Taschorema pallescens* also occurred in both seasons; Bunn (1988) described these species as multivoltine, with overlapping generations breeding all year.

Terrestrial species

Six taxa collected in this study (the ostracod ?*Mesocypris* sp. 291, the amphipods *Agilestia* sp. A and *Austrotroides pectinalis* and the three isopods) are usually regarded as terrestrial but we are confident that, with the possible exception of ?*Mesocypris* sp. 291, all were submerged in lakes, rivers or streams when collected.

In addition to West Gully and Gardner Lake, the isopod *Styloniscus australiensis australiensis* has been recorded from submerged root mats in a subterranean stream in Western Australia (B Knott, unpubl. data). The species appears to have a facultative aquatic life-history. Another isopod with the branchial morphology of a terrestrial species, *Haloniscus stepheni*, was recently found submerged in salt lakes (A J A Green, S Halse and B Knott, unpubl. data). Re-examination of the amount of time 'terrestrial' isopods spend in aquatic situations seems warranted.

Richness and endemism

The macroinvertebrate fauna of streams and rivers in southwestern Australia is depauperate in comparison to southeastern Australia (Bunn & Davies 1990). The same applies to the native fish fauna (Allen 1982, Merrick & Schmida 1984). However, this study suggested that the wetland microfauna is richer than previously recognized: there were many new records for Western Australia and, in some cases, Australia. Many of the taxa were undescribed.

Protozoan communities of inland waters of Western Australia are virtually unstudied. Foissner & O'Donoghue (1990) described five new species from a freshwater pond in Perth and Post *et al.* (1983) described 14 new species from a saline lagoon north of Perth. Taxa identified at Two Peoples Bay were all testate amoebae, the cases of which were noted whilst searching for larger microfauna. Most could be identified only to genus. It seems likely that Australia has a distinctive protozoan fauna but lack of data prevents speculation about the fauna of different regions.

Little is known of the rotifer communities of Western Australia. Koste *et al.* (1983) reviewed available records and listed 83 taxa from the southwest. Given that 21 of the 41 rotifers collected at Two Peoples Bay were not listed by Koste *et al.* (1983), it would seem that many more species remain to be found. Areas in eastern Australia of comparable size to the southwest of Western Australia have 300-500 rotifer species (R J Shiel, unpubl. data).

Many rotifers appear to be cosmopolitan or very widely-dispersed (Dumont 1983). Collections from Two Peoples Bay contained the first records of *Lecane imbricata* and *Monostyla rhopalura* for Australia (see Appendix) and at least two undescribed species (*Monostyla* sp. nov. A and *Notommata* sp. nov. A). Furthermore, several taxa (identified to genus in Appendix) resembled rotifers known from eastern Australia but had slightly different morphology. Although studies on populations from both sides of the continent are required to determine whether this represented ecotypic variation or reflected east-west divergence,

the existence of at least two, and possibly several, undescribed species in the small sample from Two Peoples Bay supports Koste *et al.*'s (1983) belief that there is a comparatively high level of endemism in the southwestern Australian rotifer fauna.

The distinctiveness and richness of the Western Australian cladoceran fauna was pointed out by Frey (1991). In revising the taxonomy of Australian species formerly assigned to the genus *Pleuroxus*, he described two new genera and four new species from southwestern Australia and suggested that there has been significant adaptive radiation compared with eastern Australia. Of the 27 cladoceran taxa collected from Two Peoples Bay, at least five species appear to be undescribed (*Biapertura* sp. M1., cf. *Pleuroxus* sp. A, Chydoridae sp. A1, Chydoridae sp. M2 and Macrothricidae gen. nov.).

The high level of endemism among calanoid copepods in Western Australia was noted by Maly & Bayly (1991). The harpacticoid copepods we collected support Hammond's (1987) suggestion that an interesting fauna awaits discovery in southwestern Australia. Canthocamptidae sp. A is possibly undescribed and the record of *Schizopera clandestina* from Gardner Lake is the first in the southern hemisphere of a species previously known only from western Europe. The occurrence of a species of *Leptomesocira* in Websters Gully is unusual: there are very few records of the genus from other than the benthos of the open sea or, less commonly, coarse sand on a marine shore (R Hammond, pers. comm.).

Most cyclopoid copepods could be identified only to genus because the taxonomy of the group is poorly known. Undescribed species occur in Western Australia (D W Morton, pers. comm.) but the level of endemism is unknown.

There are many undescribed species of ostracod in fresh and saline waters of southwestern Australia (P DeDecker & S A Halse, unpubl. data). Of taxa collected at Two Peoples Bay, the genus *Paralimnocythere* is known to be represented in Australia only by the Two Peoples Bay specimens and an undescribed species from Ellen Brook on the Swan Coastal Plain. *Gomphodella* aff. *maia* collected from Two Peoples Bay is widespread in southwestern Australia but is distinct from the eastern Australian species *G. maia* (DeDecker 1981, and pers. comm.).

Salinity and disturbance

With the exception of Gardner Lake, which becomes brackish in summer, all waterbodies sampled at Two Peoples Bay were fresh (Table 1). Furthermore, vegetation was intact around the lakes and there had been minimal impact of human activity on the aquatic systems. This is unusual in southwestern Australia, where salination as a result of land-clearing is widespread (Schofield *et al.* 1988). Many fresh waterbodies on the Swan Coastal Plain have been modified or become eutrophic (Halse 1989) and the extreme southwest of Western Australia, from Two Peoples Bay to Augusta, is the only region containing extensive areas of undisturbed wetlands.

Many species of aquatic invertebrate cannot tolerate low levels of salinity (Hart *et al.* 1991) or the extent of disturbance common on the Swan Coastal Plain (Growths *et al.* 1992; Davis *et al.* 1993). Some species in the wetlands of Two Peoples Bay have probably persisted only because the waterbodies are relatively undisturbed. It is likely the wetlands of the extreme southwest of Western Australia will be important for the future conservation of freshwater invertebrates.

Biogeography

Little is known about the biogeography of aquatic invertebrates of Western Australia but we speculate that:

(1) Rotifers and microcrustaceans, which have drought-resistant stages and poor powers of active dispersal (Dumont 1983), probably have experienced considerable radiation and, therefore, show a high degree of endemism (Frey 1991). More mobile groups, such as insects and water mites, the larvae of which are parasitic on adult insects (M Harvey, pers. comm.), demonstrate less endemism.

(2) The occurrence of several species only in southwestern Australia and Tasmania suggests there may be a biogeographic link between these regions. Shiel *et al.* (1989) recorded a highly diverse rotifer fauna from acidic lakes in western Tasmania, with a predominance of taxa now recorded primarily in the tropics. They proposed that this fauna "may have persisted in Tasmanian waters as relict populations from a time when Tasmania's climate, and that of southern Australia was tropical". Contraction in the distribution of many species is thought to have occurred when Australia experienced an arid phase approximately 18 000 year BP, during which many lakes dried and populations survived in permanent, coastal lakes (De Deckker 1986). Shiel *et al.* (1989) suggest that due to the prevailing westerly wind, lakes in coastal western Tasmania acted as refugia by remaining permanent during this arid period, and ice-free during the height of the last glaciation.

During the arid period, refugia probably also existed in coastal southwestern Australia owing to the ameliorating effects on climate of the prevailing south-westerly winds. Temperatures and the availability of water appear to have remained fairly constant over the last 30 000 years (Thorpe & Davidson 1991). It is likely that lakes on the western coast of Tasmania and southwestern coast of Western Australia today contain relicts from the eastern and western extremes of the range of a once widespread fauna.

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References

- Allen G R 1982 Inland Fishes of Western Australia. Western Australian Museum, Perth.
- Balla S A 1993 Wetlands of the Swan Coastal Plain, Vol 5. Managing Perth's Wetlands to Conserve the Aquatic Fauna. Water Authority of Western Australia, Perth.
- Bayly I A E 1982 Invertebrate fauna and ecology of temporary pools on granite outcrops in southern Western Australia. Australian Journal of Marine and Freshwater Research 33:599-606.
- Bunn S E 1988 Life histories of some benthic invertebrates from streams of the northern jarrah forest, Western Australia. Australian Journal of Marine and Freshwater Research 39:785-804.
- Bunn S E, Edward D H & Loneragan N R 1986 Spatial and temporal variation in the macroinvertebrate fauna of streams of the northern jarrah forest, Western Australia: community structure. Freshwater Biology 16:67-91.
- Bunn S E & Davies P M 1990 Why is the stream fauna of south-western Australia so impoverished? Hydrobiologia 194:169-176.
- Davis J A, Rosich R S, Bradley J S, Grown J E, Schmidt L G & Cheal F 1993 Wetlands of the Swan Coastal Plain, Vol 6. Wetland Classification on the Basis of Water Quality and Invertebrate Community Data. Water Authority of Western Australia, Perth.
- DeDeckker P 1981 Taxonomy and ecological notes of some ostracods from Australian inland waters. Transactions of the Royal Society of South Australia 105:91-138.
- DeDeckker P 1986 What happened to the Australian aquatic biota 18 000 years ago. In: Limnology in Australia (eds P DeDeckker & W D Williams) CSIRO, Melbourne, 487-496.
- DeHaan M 1987 The possible effects of peat mining on aquatic invertebrates in the Lake Muir wetlands, Western Australia. Honours thesis, Murdoch University.
- Dumont H J 1983 Biogeography of rotifers. Hydrobiologia 104:19-30.
- Foissner W & O'Donoghue P J 1990 Morphology and infraciliature of some freshwater ciliates (Protozoa: Ciliophora) from Western and South Australia. Invertebrate Taxonomy 3:661-696.
- Frey D G 1991 The species of *Pleuroxus* and of three related genera (Anomopoda, Chydoridae) in southern Australia and New Zealand. Records of the Australian Museum 43:291-372.
- Grown J O 1992 Macroinvertebrate community structure in the streams of the southern forest region of Western Australia: the influence of seasonality, longitudinal gradients and forestry activities. PhD thesis, Murdoch University.
- Grown J O & Davis J A 1991 Comparison of the macroinvertebrate communities in streams in logged and undisturbed catchments eight years after harvesting. Australian Journal of Marine and Freshwater Research 42:689-706.
- Grown J E, Davis J A, Cheal F, Schmidt L, Rosich R & Bradley S J 1992 Multivariate pattern analysis of wetland invertebrate communities and environmental variables in Western Australia. Australian Journal of Ecology 17:275-288.
- Halse S A 1989 Wetlands of the Swan Coastal Plain - past and present. In: Proceedings of the Swan Coastal Plain Groundwater Management Conference (ed G Lowe) Western Australian Water Resources Council, Perth, 105-112.
- Halse S A, Vervest R M, Munro D R, Pearson G B & Yung F H 1992 Annual waterfowl counts in south-western Australia. Technical Report 29, Department of Conservation and Land Management, Perth.
- Hart B T, Bailey P, Edwards R, Horte K, James K, McMahon A, Meredith C & Swadling K 1991 A review of the salt sensitivity of the Australian freshwater biota. Hydrobiologia 210:105-144.
- Hamond R 1987 Non-marine harpacticoid copepods of Australia. I. Canthocamptidae of the genus *Canthocamptus* Westwood s. lat. and *Fibulacamptus*, gen. nov., and including the description of a related new species of *Canthocamptus* from New Caledonia. Invertebrate Taxonomy 1:1023-1247.
- Hillman T J & Shiel R J 1991 Macro- and micro-invertebrates in Australian billabongs. Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie 24:1581-1587.
- Jaensch R P, Vervest R M & Hewish M J 1988 Waterbirds in nature reserves of south-western Australia 1981-1985. Report 30, Royal Australasian Ornithologists Union, Melbourne.
- Lane J A K & Munro D R 1983 1982 review of rainfall and wetlands in the south-west of Western Australia. Report 58, Department of Fisheries & Wildlife, Perth.
- Koste W, Shiel R J & Brock M A 1983 Rotifera from Western Australian wetlands with descriptions of two new species. Hydrobiologia 104:9-17.
- Maly E J & Bayly I A E 1991 Factors influencing biogeographic patterns of Australasian centropagid cnepepods. Journal of Biogeography 18:455-461.
- Merrick J R & Schmida G E 1984 Australian Freshwater Fishes. Biology and Management. Griffin Press Ltd, South Australia.
- Post F J, Borowitzka L J, Borowitzka M A, Mackay B & Moulton T 1983 The Protozoa of a Western Australia hypersaline lagoon. Hydrobiologia 105:95-113.
- Pusey B J & Edward D H 1990 Limnology of the southern acid peat flats, south-western Australia. Journal of the Royal Society of Western Australia 73:29-46.
- Schofield N J, Ruprecht J K & Loh I C 1988 The impact of agricultural development on the salinity of surface water resources of south-western Australia. Report WS 27, Water Authority of Western Australia, Perth.
- Shiel R J, Koste W & Tan L W 1989 Tasmania revisited: rotifer communities and habitat heterogeneity. Hydrobiologia 186/187:239-245.
- Smith G T 1985 Population and habitat selection of the Noisy Scrub-bird (*Atrichornis clamosus*), 1962 to 1983. Australian Wildlife Research 12:479-485.
- Smith, G T & Calver M C 1984 The diet of the nestling Noisy Scrub-bird *Atrichornis clamosus*. Australian Wildlife Research 11:553-558.
- Storey A W, Bunn S E, Davies P M & Edward, D H 1990 Classification of the macroinvertebrate fauna of two river systems in south-western Australia in relation to physical and chemical parameters. Regulated Rivers: Research and Management 5:217-232.
- Storey A W & Edward D H D 1989 Longitudinal variation in community structure of Chironomidae (Diptera) in two south-western Australian river systems. Acta Biologica Debrecina Oecologica Hungarica 3:315-328.
- Thorpe P M & Davidson W A 1991 Groundwater age and hydrodynamics of the confined aquifers, Perth, Western Australia. In: Proceedings of the International Conference on Groundwater in Large Sedimentary Basins, Perth, Western Australia, 1990. Conference Series 20, Australian Water Resources Council, Canberra, 420-436.

Appendix. Invertebrate species collected in streams and lakes of the Two Peoples Bay area in June 1990 and February 1991.

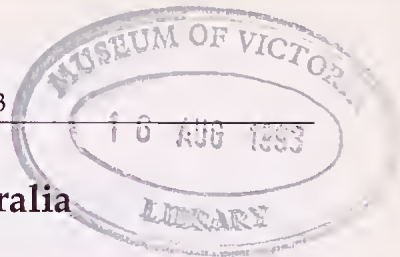
S = summer, W = winter, B = both seasons, * = sampled only in summer. Winter samples of taxa marked with * collected in September 1991. First records for Western Australia marked with *. Voucher specimen numbers are used for some undescribed species (e.g. *Biapertura* sp. M1, *Ilyodromus* sp. 255, *Macropelopia* sp. V9)

AG, Angove River; GR, Goodga River; WG, West Gully; WbG, Websters Gully; AL, Angove Lake; GL, Gardner Lake; ML, Moates Lake.

	AR	GR	WG	WbG	AL	GL	ML
PROTOZOA							
<i>Arcella</i> sp. A					*		
<i>Centropyxis</i> sp. A					*		
* <i>Diffugia acuminata</i> Ehrenberg					*		
<i>Diffugia</i> sp. A					*		
<i>Eulophia</i> sp. A					*		
* <i>Lesquerusia spiralis</i> (Ehrenberg)					*		
ROTIFERA							
<i>Bdelloida</i> sp. A					*		
<i>Brachionus</i> cf. <i>angularis bidens</i> Plate					*	*	
<i>Brachionus quadridentatus</i> Hermann					*	*	
* <i>Dipleuchlanis propatula</i> (Gosse)					*	*	
<i>Euchlanis dilatata</i> Ehrenberg					*		
* <i>Filinia</i> cf. <i>australiensis</i> Koste					*	*	
* <i>Filinia</i> cf. <i>pejleri</i> Hutchinson					*		
* <i>Filinia</i> sp. A					*		
* <i>Heterolepadella ehrenbergi</i> (Perty)					*		
<i>Keratella javana</i> Hauer					*		
<i>Keratella procurva</i> (Thorpe)					*		
<i>Keratella</i> sp. A					*		
* <i>Lecane imbricata</i> Carlin					*	*	
* <i>Lecane</i> cf. <i>ohioensis</i> (Herrick)					*	*	
* <i>Lecane signifera</i> (Jennings)					*		
* <i>Lepadella rottenburgi</i> (Lucks)					*		
* <i>Lepadella triptera</i> (Ehrenberg)					*		
<i>Lepadella</i> sp. A					*		
* <i>Macrochaetus collinsi</i> (Gosse)					*		
<i>Monommata</i> sp. A					*		
<i>Monostyla bulla</i> (Gosse)					*	*	*
<i>Monostyla hamata</i> (Stokes)					*	*	
<i>Monostyla lunaris</i> Ehrenberg					*		
* <i>Monostyla crenata</i> (Harring)					*	*	
* <i>Monostyla furcata</i> Murray					*	*	
* <i>Monostyla quadridentata</i> (Ehrenberg)					*	*	
* <i>Monostyla rhophalura</i> Harring & Myers					*	*	
* <i>Monostyla</i> sp. nov. A					*		
* <i>Notommata</i> sp. nov. A					*	*	
<i>Platylas quadricornis</i> (Ehrenberg)					*		
* <i>Testudinella amphiora</i> Hauer					*		
<i>Testudinella insinuata</i> Hauer					*		
<i>Testudinella nr patina</i> (Hermann)					*	*	
* <i>Testudinella tasmaniensis</i> Koste & Shiel					*	*	
<i>Trichocerca elongata</i> (Gosse)					*	*	
<i>Trichocerca pusilla</i> Jennings					*	*	
* <i>Trichocerca rattus carinata</i> (Ehrenberg)					*	*	
* <i>Trichocerca rattus cristata</i> (Harring)					*	*	
<i>Trichocerca</i> sp. A1					*	*	
<i>Trichocerca</i> sp. A2					*	*	
<i>Trichotria tetractis</i> (Ehrenberg)					*	*	
NEMATODA							
	S	S	B	B	B		
MOLLUSCA							
GASTROPODA							
PULMONATA							
Ancyliidae							
<i>Ferrissia petterdi</i> (Johnston)		W	B		B		W
Planorbidae							
<i>Physastra</i> sp. A					B		
ANNELIDA							
OLIGOCHAETA							
	B	B	B	W	B	B	B
ARTHROPODA							
ARACHNIDA							
ORIBATIDA							
					W	B	B
HYDRACARINA							
Arrenuridae							
<i>Arrenurus</i> sp. A			S				
<i>Arrenurus</i> sp. B			S				
Oxidae							
<i>Flabellifrontipoda</i> sp. A		W					
<i>Limnochares australica</i> Lundblad					S		
<i>Oxus</i> sp. A					W	B	B
<i>Frontipoda</i> sp. A		S					
Unionicolidae							
<i>Koenikea</i> sp. A					B		
<i>Newmania</i> sp. A		S					
Hygrobatidae							
<i>Corticarus</i> sp. A		W					

	AR	GR	WG	WbG	AL	GL	ML
<i>Gretacarus</i> sp. A						S	S
<i>Coaustraliobates</i> sp. A		S					
Halacaridae							
<i>Halacaridae</i> sp. A						W	
<i>Soldanellonyx</i> sp. A					S		
CRUSTACEA							
CLADOCERA							
Sididae							
<i>Latonopsis</i> cf. <i>brehmi</i> Petkovski							S
Chydoridae							
<i>Alonella</i> cf. <i>clathratula</i> Sars							S
<i>Biapertura</i> cf. <i>affinis</i> (Leydig)							W
<i>Biapertura</i> cf. <i>rigidicaudis</i> Smirnov						W	
* <i>Biapertura</i> cf. <i>setigera</i> (Brehm)					S		S
* <i>Biapertura</i> sp. M1							B
* <i>Camptocercus</i> cf. <i>australis</i> Sars							S
* <i>Chydorus</i> sp. A					B	W	S
<i>Dunhevedia crassa</i> King						W	
<i>Ephemeropeporus barroisi</i> Frey s. l.						S	
* <i>Euryalona</i> cf. <i>orientalis</i> (Daday)					W		
* <i>Graptoleberis</i> cf. <i>testudinaria</i> (Fischer)							W
* <i>Monope reticulata</i> (Henry)							S
*cf. <i>Pleuroxus</i> sp. A					W		W
* <i>Rhynchochydorus nr australiensis</i> Smirnov & Timms					S		
* <i>Chydoridae</i> sp. A1					B		
* <i>Chydoridae</i> sp. M2							S
Macrothricidae							
* <i>Echinisca</i> sp. A						W	
* <i>Ilyocryptus</i> sp. A						W	
<i>Macrothrix</i> cf. <i>breviseta</i> Smirnov & Timms						B	
* <i>Neothrix armata</i> Gurney						B	
* <i>Macrothricidae</i> gen. nov. A						S	
Daphniidae							
<i>Scapholeberis nr kingi</i> Sars						S	S
<i>Simocephalus exspinosus australiensis</i> (Dana)		S					
<i>Simocephalus</i> sp. A						W	
Bosminidae							
<i>Bosmina meridionalis</i> Sars						W	B
<i>Bosmina</i> sp. A						W	
OSTRACODA							
<i>Ostracoda</i> sp. 287						S	
Cyprididae							
<i>Cypretta baylyi</i> McKenzie						B	W
* <i>Ilyodromus</i> sp. 255		B				S	
<i>Kennethia cristata</i> De Deckker						B	W
<i>Alboa worooa</i> DeDeckker						S	W
? <i>Mesocypris</i> sp. 291					S		
Darwinulidae							
? <i>Darwinula</i> sp. A						W	S
Limnocytheridae							
<i>Gomphodella aff. maia</i> DeDeckker						B	B
<i>Limnocythere mowbrayensis</i> Chapman						W	
* <i>Paralimnocythere</i> sp. nov.						B	S
Candonidae							
<i>Candonopsis tenuis</i> (Brady)						W	W
COPEPODA							
Centropagidae							
<i>Calamoecia attenuata</i> (Fairbridge)						B	B
<i>Calamoecia tasmanica</i> Smith s. l.							S
<i>Calamoecia tasmanica subattenuata</i> (Fairbridge)						B	W
<i>Gladioferens imparipes</i> Thomson						S	B
Cyclopidae							
<i>Eucyclops australiensis</i> Morton		S				S	S
<i>Halicyclops</i> sp. A							S
<i>Microcyclops</i> sp. A						W	W
<i>Thermocyclops</i> sp. A						B	W
<i>Macrocylops albidus</i> (Jurine)		S				W	W
<i>Paracyclops chiltoni</i> (Thomson)		S					B
<i>Paracyclops</i> sp. A							W
Canthocamptidae							
* <i>Canthocamptidae</i> sp. A						W	W
<i>Canthocamptidae</i> sp. 15						S	S
<i>Canthocamptidae</i> sp. 16							S
<i>Leptomesochra</i> sp. A						S	
<i>Onychocamptus bengalensis</i> (Sewell)							S
* <i>Onychocamptus clathamensis</i>						W	W
<i>Nitocra</i> sp. A							S
* <i>Schizopera clandestina</i> (Klie)							B
DECAPODA							
Parastacidae							
<i>Cherax plebejus</i> (Hess)		B	W				W
<i>Cherax quinquecarinatus</i> (Gray)		B	S			W	S
<i>Cherax tenuimanus</i> (Smith)		W	B			W	S
Palaemonidae							
<i>Palaemonetes australis</i> Dakin		B				B	B

	AR	GR	WG	WbG	AL	GL	ML		AR	GR	WG	WbG	AL	GL	ML
AMPHIPODA															
Ceinidae															
Austrochiltonia subtenuis Hurley					W	B	B				S				
Gammaridae															
Perthia branchialis (Nicholls)	B	S			B		S								W
Perthia acutitelson Straskraba		W													S
Uroctena setosa Nicholls			B											W	
Talitroidea															
Agilestia sp. A			S	S					S	S					
Austrotroides pectinalis Friend		S							S		S	S			
ISOPODA															
Philosciidae															
?Laevophiloscia sp. A			S												
?Plymophiloscia sp. A			S			W							W	W	
Styloniscidae															
Styloniscus australiensis australiensis Vandel			S			W									
INSECTA															
MEGALOPTERA															
Chaulioididae															
Archichauliodes cervulus Theischinger	B														
LEPIDOPTERA															
Lepidoptera sp. B		S													
DIPTERA															
Simuliidae															
Cnephia tonnoiri tonnoiri Drummond	B	W	W	W											
Austrosimulium furiosum (Skuse)	B	W													
Culicidae															
Aedes sp. A						W									
Anopheles annulipes Walker			S												
Culex australicus Dobrotworsky & Drummond			S	S											
Culex globocoxitus Dobrotworsky						W									
Chironomidae															
Tanypodinae															
Coelopomyia pruinosa Freeman							S								
Paramerina levidensis (Skuse)	S	S	B	B	S	W	B								
Macropelopia dalyupensis (Freeman)					W		S								
Macropelopia sp. V9	W														
?Ablabesmyia sp. V10	B														
Tanypodinae sp. V20			S												
Orthoclaadiinae															
Corynoneura ?scutellata Winnertz						W									
Cricotopus annuliventris (Skuse)	B	B	W	B											
Stictocladus uniserialis Freeman		W													
Nanocladus sp. VCD7							W								
Thienemanniella sp. V19	B	W	W	W	W	W	B								
Limnophyes pullulus (Skuse)	S			B	W	W	B								
?Limnophyes sp. V31	W						S								
Orthoclaadiinae sp. V11	B	B		W											
Orthoclaadiinae sp. VTPB1					W	W									
Orthoclaadiinae sp. VTPB2					S										
Orthoclaadiinae sp. VTPB3	S														
Orthoclaadiinae sp. V59	B														
Orthoclaadiinae sp. A					W	W									
Chironominae															
Cladopelma curtivalva (Kieffer)			S		S		S								
?Harnischia sp. VTPB4			S				S								
Polypedilum sp. V3	B	S	B	W	W		B								
Polypedilum sp. V33	B			B											
Polypedilum sp. A						S									
Procladius paludicola Skuse		S			S	S	S								
Riethia sp. V4	B	B	S				S								
Riethia sp. V5	B		B	S			S								
Cladotanytarsus ? mancus (Walker)						S	S								
Tanytarsus sp. V6	B	B	W	B	W	B									
Tanytarsus sp. A					S		S								
Tanytarsus sp. B					S										
Stempellina ?australiensis Freeman	B	S	B	S											
?Paratendipes sp. V12	W														
Rheotanytarsus sp. V18	S	W				S									
Cryptochironomus griseidorsum Kieffer		B		S			W								
Stenochironomus sp. V27	B														
Chironomus aff. alternans Walker	S		S												
Tanytarsini sp. A						W	W								
Chironomini sp. V21	S														
Dicrotendipes sp. V47		S													
Tipulidae															
Limoniinae sp. A	S		B	B		W									
Limoniinae sp. B			B	W											
?Pedicia sp. A			W	W											
Tipulinae sp. A	S		B	S											
Ceratopogonidae															
Ceratopogonidae sp. A	W		W	B											
Ceratopogonidae sp. B		B	S	B	W	B	W								
Ceratopogonidae sp. C						W									
Ceratopogonidae sp. D							W								
Ceratopogonidae sp. F				S											
Ceratopogonidae sp. G							S								
Ceratopogonidae sp. K															
Ceratopogonidae sp. O															
Stratiomyidae															
Stratiomyidae sp. A															W
Stratiomyidae sp. B															S
Dolichopodidae															
Dolichopodidae sp. A													W		
Empididae															
Empididae sp. A		S	S						S	S					
Empididae sp. B		S		S	S				S		S	S			
ODONATA															
ZYGOPTERA															
Coenagrionidae															
Ischnura sp. A											S				
Ischnura aurora (Brauer)											S				
ANISOPTERA															
Aeschnidae															
Austroaeschna anacantha Tillyard		B	B	B	B										S
Corduliidae															
Lathrocordulia metallica Tillyard		S													
Cordulidae sp. A (immature)		W													
Hemicordulia tau Selys			S												
Gomphidae															
Austrogomphus collaris Hagen			B												
Libellulidae															
Diplacodes haematodes (Burmeister)														W	
Synthemidae															
Synthemis macrostigma occidentalis Tillyard													W		
Synthemis cyanitincta Tillyard		S													
HEMIPTERA															
Veliidae															
Veliidae sp. A														W	
Corixidae															
Agraptocorixa sp. A														S	
Micronecta robusta Hale														W	
EPHEMEROPTERA															
Leptophlebiidae															
Nyungara bunni Dean		B													
Bibulnena kadjina Dean			W	B	B										
Neboissophlebia occidentalis Dean		S	S												
Caenidae															
Tasmanocoenis tillyardi (Lestage)			B										W		
PLECOPTERA															
Gripopterygidae															
Newmanoperla exigua (Kimmins)			W												
Gripopterygidae sp. A (immature)				W											
TRICHOPTERA															
Hydropsychidae															
Smicrophylax australis (Ulmer)		B	B												
Ecnomidae															
Ecnomina sciudens/trulla/merga group		B													
Ecnomus pansus/turgidus complex			B	W											S
Leptoceridae															
Condocerus aptus Neboiss		B											B		
Lectrides parilis Neboiss		B	S	B										S	S
Oecetis spp.			S											S	S
Triplectides sp. A		W												W	W
Triplectides australis Navas															B
Notoperata tenax Neboiss		S													
Hydroptilidae															
Hellyethira malleoforma Wells			S											S	S
Oxyethira retracta Wells		W	S												
Maydenoptila ?rupina Neboiss			W												
Hydroptila losida Mosely			S												
Hydrobiosidae															
Taschorema pallescens (Banks)		B	B	B	B										
Polycentropodidae															
Plectrocnemia ?exima Neboiss															S
COLEOPTERA															
Dytiscidae															
Antiporus femoralis (Boheman)															S
Lancetes lanceolatus (Clark)														W	W
Liodessus dispar (Sharp)														W	W
Megaporus howitti (Clark)															
Megaporus solidus (Sharp)			S												
Necterosoma darwini (Babington)													B		
Necterosoma sp. B (larva)			S										S		
Rhantus suturalis (MacLeay)													W		
Sternopriscus browni Sharp															
Sternopriscus sp. A														S	
Platynectes decempunctatus (Fabricius)				S											
Helodidae															
Helodidae sp. A		S	S	B	B		W								
Hydrophilidae															
Hydrophilidae sp. I				S											
Number of Species															
		53	55	40	43	96	72	85							



Recent Advances in Science in Western Australia

Life Sciences

An analysis of the distributions of terrestrial mammals, birds and reptiles for north-western Australia by J Woinarski, of the Conservation Commission of the Northern Territory / CSIRO Division of Wildlife and Ecology, shows that diversity is highest in coastal, high rainfall zones compared to transitional and inland, low rainfall zones. The mammal/bird/reptile assemblages of the coastal zone are well represented by the 58 nature reserves of the region, but transitional and inland assemblages are poorly represented.

Woinarski J C Z 1992 Biogeography and conservation of reptiles, mammals and birds across north-western Australia: an inventory and base for planning an ecological reserve system. *Wildlife Research* 19:665-705.

Differences in foliar nutrient levels for two co-dominant eucalypts at sites in western and eastern Australia, measured by J Majer and S Ganeshanandam (Curtin University of Technology) and H Recher (University of New England) reveal differences that are consistent with trends in the abundance and diversity of foliage arthropods and foraging use of trees by birds.

Majer J D, Recher H F, & Ganeshanandam S 1992 Variation in foliar nutrients in *Eucalyptus* trees in eastern and Western Australia. *Australian Journal of Ecology* 17:383-393.

An extensive 2 year study by I Abbott and co-workers from the Research Centre, CALM, of arthropod jarrah crown fauna in 7500 km² centred on Manjimup revealed more than 396 species, predominated by leaf chewer, sapsucker and predator guilds. There was no apparent single pattern of organization or predictable assemblages of these jarrah foliage invertebrates.

Abbott I, Burbidge T, Williams M, & Van Heurck P 1992 Arthropod fauna of jarrah (*Eucalyptus marginata*) foliage in mediterranean forest of Western Australia: spatial and temporal variation in abundance, biomass, guild structure and species composition. *Australian Journal of Ecology* 17:263-274.

The history of the rodent fauna of Australia has been examined by C Watts and co-workers, of the South Australian Museum and University of New England (Northern Rivers). Albumin evolution, determined using microcomplement fixation, has not occurred in a clock-like manner. The genera *Conilurus*, *Leporillus* and *Mesembriomys* form a monophyletic group, as do *Notomys*, *Mastacomys* and *Pseudomys*. The genus *Mastacomys* was synonymised with *Pseudomys*, which is polyphyletic.

Watts C H S, Baverstock P R, Birrell J, & Krieg M 1992 Phylogeny of the Australian rodents (Muridae): a molecular approach using microcomplement fixation of albumin. *Australian Journal of Zoology* 40:81-90.

The impact of fire upon the predominant frogs of *Banksia* woodland has been examined by M Bamford, near Perth. Recent fire did not greatly affect the numbers of *Heleioporus eyrei*, but did decrease the numbers of *Limnodynastes dorsalis*, and to a lesser extent the numbers of *Myobatrachus gouldii*.

Bamford M J 1992 The impact of fire and increasing time after fire upon *Heleioporus eyrei*, *Limnodynastes dorsalis* and *Myobatrachus gouldii* (Anura: Leptodactylidae) in *Banksia* woodland near Perth, Western Australia. *Wildlife Research* 19:169-178.

Earth Sciences

R Salama and co-workers of the Division of Water Resources, CSIRO (Wembley), describe the geochemical evolution of Lake Deborah East, a playa lake with a thick salt crust underlain by stratified lacustrine deposits of unconsolidated evaporite minerals intercalated with clay and sand; the sequence is of Late Tertiary and Quaternary age. Evidence from the salt budget of prolonged arid periods, with no salt addition, is consistent with other lines of evidence for frequent dry periods during the last 400,000 years.

Salama R, Barber C, Hosking J, & Briegel D 1992 Geochemical evolution of Lake Deborah East, prototype salt lake in the relict drainage of the Yilgarn River of Western Australia. *Australian Journal of Earth Sciences* 39:577-590.

I Williams of the Geological Survey of Western Australia provides the first description of a newly recognised 900-600 Ma Proterozoic sedimentary basin in the Little Sandy Desert region east and southeast of Newman. The Savory Basin is situated between the Pilbara and Yilgarn Cratons and unconformably overlies the eastern part of the Middle Proterozoic Bangemall Basin, and is unconformably overlain by Phanerozoic rocks of the Officer Basin. The Basin fill is predominantly arenaceous and includes an important geological sequence, biostratigraphically significant stromatolitic dolomites, and evaporite occurrences.

Williams I R 1993 Geology of the Savory Basin, Western Australia. *Western Australian Geological Survey, Bulletin* 141.

In a valuable study of the Menzies-Kambalda area of the Archaean Yilgarn Craton which has yielded large quantities of gold, W Witt of the Geological Survey of Western Australia describes structurally-controlled gold mineralization in a wide variety of host rocks and structural settings. Mineralized structures in the host rocks, which are predominantly Fe-enriched basalt and fractionated zones of mafic to ultramafic sills, can generally be related to the latest events in the regional deformation history of the greenstone belt or forceful emplacement of contemporaneous granitoid intrusions.

Witt W K 1993 Lithological and structural controls on gold mineralization in the Archean Menzies-Kambalda area, Western Australia. *Australian Journal of Earth Sciences* 40:65-86.

Relict channels in three representative dryland salinized wheatbelt catchments were identified by R Salama and co-workers of the Division of Water Resources, CSIRO (Wembley) using aerial photographs. These relict channels generally have a higher salinity than other areas in the catchment and downstream, and have an important role in the storage and redistribution of salt.

Salama R B, Farrington P, Bartle G A, & Watson G D 1993 The role of geological structures and relict channels in the development of dryland salinity in the wheatbelt of Western Australia. *Australian Journal of Earth Sciences* 40:45-56.

As part of a revision of fossil floras in Western Australia, S McLoughlin of the University of Western Australia considers the systematics, morphology, and distribution of newly collected sphenophyte fossils from the Collie and Irwin Coal

Measures. Symmetrical *Sphenophyllum* species were predominant in the Early Permian whereas bilaterally symmetrical *Trizygia* or bifid-leaved *Benlightfootia* species dominated the Late Permian.

McLoughlin S 1992 Permian sphenophytes from the Collie and Perth Basins, Western Australia. Review of Palaeobotany and Palynology 75:153-182.

This study of goniatite (cephalopod) faunas in Western Australia, by R Becker, M House and W Kirtgasser (Southampton University and State University of New York), provides an important contribution to world-wide stratigraphic correlations. Their new goniatite classifications of the Frasnian reef and detailed zonations for the Canning Basin provide a framework for analysis of facies movements and recognition of several international eustatic sea-level changes.

Becker R T, House M R, & Kirtgasser W T 1992 Devonian goniatite biostratigraphy and timing of facies movements in the Frasnian of the Canning Basin, Western Australia. In: High Resolution Stratigraphy (eds E A Hailwood & R B Kidd) Geological Society Special Publication 70, 293-321.

A special issue of Precambrian Research, edited by T Blake and A Meakins of the University of Western Australia, discusses some recent developments in Archaean and Early Proterozoic geology of the Pilbara region. The editorial preface sets the scene for a new approach to Early Precambrian geology, and the eleven papers provide valuable debate on topics including stratigraphy, geochronology, sedimentology-volcanology, plutonic rocks and tectonics of the granite-greenstone terrain and the Hamersley Province.

Blake T S & Meakins A 1993 Archaean and Early Proterozoic geology of the Pilbara Region, Western Australia. Precambrian Research, Special Issue 60, 1-359.

Physical Sciences

A group of physicists, chemists and electronic engineers at Murdoch University and The University of Western Australia have used Fourier transform infra-red spectroscopy to study how temperature affects the nature of bonding in thin films of hydrogenated amorphous silicon, an important photovoltaic material. Hydrogen was found to evolve from near-surface and bulk sites at different temperatures, and the bonding of contaminant oxygen and nitrogen moieties in the silicon network also undergo changes with temperature.

Talukder G, Cornish J C L, Jennings P, Hefter G, Jain M, Robins J L & Livingstone J 1993 Annealing effects on hydrogen, oxygen and nitrogen bonding in sputtered a-Si network. Thin Solid Films 223:167-172.

J Williams from The University of Western Australia and M Kumar and A Stelbovics of Murdoch University report measurements and associated theory for the angular correlations of sequential cascading photons for an atomic system (hydrogen) in which a scattering plane is defined. The measured angular correlations and the derived multipole moments show reasonable agreement with various theoretical models

Williams J F, Kumar M & Stelbovics A T 1993 Angular correlations between sequential cascading photons from $n=3$ atomic hydrogen. Physical Review Letters 70:1240-1243.

Physicists at Murdoch University show by calculation that the experimentally difficult Auger Electron Coincidence spectroscopy is better performed using X-ray excitation, although it is technically feasible using electron excitation.

Stelbovics A T, Todd B D, Thurgate S M & Lohmann B 1992 Limits to Auger-electron core-loss electron coincidence spectroscopy. Surface Science 278:193-201.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA).

Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. Papers in refereed journals, or books, chapters and reviews will be accepted. Abstracts from conference proceedings will not be accepted. Please submit short (2-3 sentence) summaries of recent papers, together with a copy of the title, abstract and authors' names and addresses, to the Hon Editor (c/o Western Australian Museum) or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc Prof G Hefter (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters and suggest potential reviewers or respondents to your letter.

I wish to thank Associate Professor John Webb for his past service on the Publications Committee, and welcome Associate Professor Glenn Hefter (School of Mathematical and Physical Sciences, Murdoch University) as the new member of the Publications Committee representing the Physical Sciences. P C Withers, Hon Editor, Journal of the Royal Society of WA.

Foraging strategies and defence mechanisms of termite species (Isoptera) in the Western Australian wheatbelt.

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Abstract

This study investigated the relationship between foraging strategies (reflecting exposure to predation) and mechanisms of defence for termite species in the Western Australian wheatbelt. Of 38 species studied, 17 were primarily harvesters (facing presumptive high levels of predation). All harvester species defended themselves with abundant soldiers using either chemicals (*Nasutitermitinae*), or a combination of chemicals and prominent mandibles (*Drepanotermes* sp., *Amitermes neogermanus*). Of 21 wood-eating species (facing presumptive lower levels of predation), the majority (71 %) relied on the mandible defences of relatively rare soldiers. Exceptions were wood-eating *Coptotermes* and *Schedorhinotermes* (*Rhinotermitidae*), and *Nasutitermes* and *Occasitermes* (*Nasutitermitinae*), which had more numerous soldiers with either a mixed chemical-mandibulate defence (*Rhinotermitidae*), or a chemical defence (*Nasutitermitinae*). Such defences are consistent with the defences of the rhinotermitids and nasutitermitids in general, regardless of foraging strategy. The relationship between predation risk and mechanism of defence is best exemplified by the endemic harvester genus *Drepanotermes*, which has evolved from the almost cosmopolitan, predominantly wood-eating, *Amitermes*. By filling the large harvester niche in arid and semi-arid Australia, *Drepanotermes* appears to have evolved large size in both workers and soldiers, and an abundant soldier caste displaying prominent mandibles as well as an effective means of chemical defence. The observed relationship between foraging strategies and defence mechanisms resembles observations made on South American species but does not necessarily apply to the termites in general. It also does not necessarily imply a causal relationship between foraging strategy and mechanism of defence. Potentially profitable areas of future research are identified.

Introduction

The diet of termites is often complex but consists principally of cellulose in various forms, be it living, dead but sound, or decomposed vegetation (including dung), humus or soil, or various combinations of the above (Wood 1978). However, from the view of susceptibility to predation, what is more important to termites than what they eat is how they obtain their food.

As in most organisms, foraging is associated with some risk of being eaten. Animals reduce the risk of predation by a variety of strategies such as choosing appropriate places and times for foraging, or by evolving morphological or chemical adaptations for defence. Defence strategies in termites are either mandibulate where soldiers are equipped with large mandibles (Deligne 1965); chemical, where secretions may be toxic, sticky or of repulsive odour (Quennedey 1975); or a combination of chemicals and mandibles (Blum *et al.* 1982). Most studies have emphasized chemical types of defence (see Prestwich 1988 for a review), as have most Australian investigations (Moore 1969, McMahan 1974, Eisner *et al.* 1976). Mandibulate, chemical and mixed chemical-mandibulate defence strategies are also prevalent in the termites of the Western Australian wheatbelt (Abensperg-Traun 1988, Abensperg-Traun *et al.* 1991).

Two broad termite foraging strategies are apparent. (1) Harvesting grass or other plant debris on the soil surface where exposure to predators such as ants and lizards is high; (2) *in situ* consumption of wood. By foraging within their

food source, to which predators are likely to have restricted access, such termites may experience lower levels of predation. If termites are as well defended as they need to be for the successful exploitation of such variably hostile foraging niches, one might expect termites that exploit such different niches to also differ in their mechanisms of defence.

Studies of the relationships between termite foraging strategies and their mechanisms of defence are scarce. Coles de Negret & Howse (1983) found that defence type corresponds with levels of predation for termites from parts of Brazil. Heavily predated harvester species have abundant soldiers with chemicals, whereas lightly-predated non-harvesters have few mandibulate soldiers. The relationship between foraging strategy and mechanism of defence in Australian termites has not been examined. Using the termites from the Western Australian wheatbelt, the present study tests two predictions: (1) harvester termites are heavily defended; (2) wood-eaters are lightly defended.

Study Area and Methods

Observations were made in Durokoppin (31°24'S, 117°45'E) and Kodj Kodjin (31°27'S, 117°47'E) Nature Reserves of the Western Australian wheatbelt during a study of the foraging ecology of the echidna from 1987 to 1989 (Abensperg-Traun 1990). Termite colonies were sampled in a variety of microhabitats (soil, timber, mounds), and observations regarding foraging strategy (harvesting, wood-eating) and defence mechanism were noted. Estimated numbers of colonies sampled are given for respective species. The

foraging strategy of wheatbelt termites has been discussed in earlier papers, as have been characteristics of the study area such as climate, vegetation and soils (Abensperg-Traun 1988, Abensperg-Traun 1991, Abensperg-Traun & De Boer 1990, Abensperg-Traun *et al.* 1991). By examining termites in the very broad harvester vs. non-harvester categories, I ignore potentially important, but unknown differences in the foraging strategies of individual species.

Defence mechanisms (chemical, mandibulate or mixed chemical-mandibulate) of the study species are based largely on published data which are comprehensive for the majority of taxa discussed. For instance, all *Nasutitermitinae* (*Tumulitermes*, *Nasutitermes*, *Occasitermes*) have chemical defence (Prestwich 1988), whereas *Coptotermes*, *Schedorhinotermes* and *Drepanotermes* combine large mandibles with chemical secretions (Moore 1969, Quennedey 1975; Blum *et al.* 1982). My observations on soldier defence were directed at detecting chemical secretions at sampling time. Droplets of soldier secretions from the fontanelle, an opening on the forehead, are either clearly visible (when carried between the mandibles, or after solidifying when placed into 75 % ethanol), or are apparent by odour. The abundance of termite soldiers for respective species at collection time was ranked from 1 (scarce) to 4 (abundant) rather than counted because reliable, accurate caste ratios are difficult to obtain, particularly for rare species, and generally require destructive methods such as the excavation of the entire colony. The approximations as given here are sufficient for the purpose of the present study. Mean head capsule widths of soldiers and workers, as a measure of body size, were determined from five specimens for each study species. Only those species are discussed for which adequate foraging and defence data are available.

Results

Harvester termites

Numbers of colonies of harvester termites sampled range from < 20 colonies for rare *Tumulitermes* sp. to > 100 for three *Drepanotermes* sp. and *Amitermes neogermanus* (Table 1). All harvester termites were heavily defended, upholding the study prediction. Of the 38 species studied (Table 1), 12 *Tumulitermes* sp., four *Drepanotermes* sp. and *Amitermes neogermanus* (Termitidae) were harvesters, and all possessed a chemical defence with either small but very abundant soldiers (*Tumulitermes* sp.) or a mixed chemical-mandibulate defence with abundant but larger soldiers (*Drepanotermes* sp.) (Fig 1). Harvesters made up 45 % of the species studied, although three species also ate wood. Defence in *Tumulitermes* soldiers (indeed in all *nasutitermitids*) involved the shooting of a sticky thread from the nasus (Fig 2A). Similar to *Drepanotermes* sp., *Amitermes neogermanus* soldiers readily secreted a droplet of clear fluid from the fontanelle, which was carried between the mandibles. However, the secretion was only mildly odorous, unlike that of *Drepanotermes* soldiers which is strong, reminiscent of oranges. The workers and soldiers of the endemic obligate harvester *Drepanotermes* sp. were larger than their caste equivalents of the predominantly wood-eating *Amitermes* from which they originally evolved (Fig 1).

Wood-eaters

Numbers of colonies of wood-eaters sampled (Table 1) range from < 10 colonies (e.g. *Amitermes heterognathus*) to > 100 colonies (e.g. *Coptotermes acinaciformis*). Of the 21 termite species known to be predominantly wood-eating, 15 species (71 %) were lightly defended, depending on mandibulate soldiers for colony defence (Table 1). Such soldiers were both intermediate in size (Fig 1), and rare (Table 1). Their mandibles (Fig 2) were either short and stout (*Amitermes* sp., *Coptotermes* sp., *Heterotermes* sp., *Microcerotermes* sp., *Schedorhinotermes* sp.), or long and slender (*Ephelotermes argutus*, *Paracaprithermes kraepelini*, *Xylochomitermes occidialis*). Species that were more heavily defended, and thus did not uphold the study prediction, had either more numerous, larger soldiers with a mixed chemical-mandibulate defence (*Rhinotermitidae*), or very abundant, but small soldiers with a chemical defence (*Nasutitermitinae*). *Coptotermes* soldiers secreted a droplet of milky fluid when disturbed. Chemical defence in *Schedorhinotermes* was not detected. A single soldier each of the common wood-eaters *A. obeuntis* (> 100 colonies sampled), *A. dentosus* (> 50 colonies) and *A. calabyi* (> 50 colonies), respectively, was observed to secrete chemicals from the fontanelle at collection time; their secretions solidified into a whitish mass when placed into 75 % ethanol.

Discussion

Harvesters

As predicted, all harvester termites were heavily defended. *Tumulitermes* sp. soldiers have evolved the highly specialized chemical defence (typical, and exclusive to *Nasutitermitinae*), of squirting a viscid secretion from their nozzle-like frontal gland (Fig 2A). Soldiers thus need not make physical contact with the predator to transmit the chemical. The soldiers are very small (Fig 1), each weighing as little as 1 mg fresh weight (Abensperg-Traun 1990), but (as in all species of *Nasutitermitinae*) comprise a significant proportion of the colony population (Haverty 1977). Reliable soldier: worker ratio estimates for Australian "nasute" termites (species in which the head-capsule forms a nasus) are limited to wood-eating *Nasutitermes exitiosus* in which the natural proportion of soldiers is estimated at ~ 15 % (Moore 1969); this is within the upper range of soldier:worker ratios of known species (Haverty 1977).

Gay & Calaby (1970) state that all species of *Tumulitermes* are harvesters. Evidence from the Western Australian wheatbelt supports this, although some species have a mixed diet of harvested material and wood, eaten *in situ* (Table 1). There are no published soldier:worker ratio estimates for harvester *Tumulitermes* sp. For one of its southern African ecological equivalents, the harvester *Trinervitermes trinervoides* (*Nasutitermitinae*), soldiers make up ~ 32 % of the foraging termites, which is significantly higher than their proportion within the nest (Skaife 1955, Richardson 1987).

Other (non-nasute) harvesters were also heavily defended by combining prominent mandibles with chemical secretions of abundant soldiers. They included four species of *Drepanotermes* and *A. neogermanus*. All known species of *Drepanotermes* are obligate harvesters (Watson & Perry 1981). *Amitermes neogermanus* is predominantly a harvester (storing

Table 1.
Foraging strategies and defence mechanisms of
termite species in the Western Australian wheatbelt.

TERMITE SPECIES	FORAGING STRATEGY	DEFENCE MECHANISM			SOLDIER ABUNDANCE
		Mandi- bulate	Chemical	Mixed chemical- mandibulate	
Rhinotermitidae					
<i>Coptotermes aciuaciformis</i> Froggatt (>100)	W			x	2
<i>Coptotermes frenchi</i> Hill (>50)	W			x	2
<i>Heterotermes occiduus</i> Hill (>100)	W	x			2
<i>Heterotermes paradoxus</i> Froggatt (>50)	W	x			2
<i>Schedorhinotermes actuosus</i> Hill (<10)	W			x	2
<i>Schedorhinotermes reticulatus</i> Froggatt (>100)	W			x	2
Termitidae					
<i>Amitermes calabyi</i> Gay (>50)	W	x			1
<i>Amitermes capito</i> Hill (>20)	W	x			1
<i>Amitermes dentosus</i> Hill (>50)	W	x			1
<i>Amitermes hartmeyeri</i> Silvestri (>50)	W	x			1
<i>Amitermes heterognathus</i> Silvestri (< 10)	W	x			1
<i>Amitermes neogermanus</i> Hill (>100)	H, W			x	3
<i>Amitermes obeuntis</i> Silvestri (>100)	W	x			1
<i>Amitermes perarmatus</i> Silvestri (>50)	W	x			1
<i>Amitermes westraliensis</i> Hill (<10)	W	x			1
<i>Drepanotermes gayi</i> Watson & Perry (>20)	H			x	4
<i>Drepanotermes perniger</i> Froggatt (>100)	H			x	4
<i>Drepanotermes rubriceps</i> Froggatt (>100)	H			x	4
<i>Drepanotermes tanninensis</i> Hill (>100)	H			x	4
<i>Ephelotermes argutus</i> Hill (>100)	W	x			1
<i>Microcerotermes distinctus</i> Silvestri (>50)	W	x			1
<i>Microcerotermes newmani</i> Hill (>100)	W	x			1
<i>Paracapritermes kraepelinii</i> Silvestri (>100)	W	x			1
<i>Xylochomitermes occidialis</i> Gay (>100)	W	x			1
Nasutitermitinae					
<i>Nasutitermes exitiosus</i> Hill (>100)	W		x		4
<i>Occasitermes occasus</i> Silvestri (>50)	W		x		4
<i>Tumulitermes comatus</i> Hill (>20)	H		x		4
<i>Tumulitermes dalbiensis</i> Hill (>100)	H		x		4
<i>Tumulitermes peracutus</i> Hill (>100)	H, W		x		4
<i>Tumulitermes petilus</i> Hill (>100)	H, W		x		4
<i>Tumulitermes</i> sp. "AI" (<20)	H		x		4
<i>Tumulitermes</i> sp. "AJ" (<20)	H		x		4
<i>Tumulitermes</i> sp. "AK" (<20)	H		x		4
<i>Tumulitermes</i> sp. "B" (<20)	H		x		4
<i>Tumulitermes</i> sp. "MT" (<20)	H		x		4
<i>Tumulitermes</i> sp. "O" (<20)	H		x		4
<i>Tumulitermes</i> sp. "V" (<20)	H		x		4
<i>Tumulitermes</i> sp. "W" (<20)	H		x		4

Code initials for undescribed species as in Abensperg-Traun (1988, 1991) and Abensperg-Traun & De Boer (1990). W = wood-eating, H = harvesting. Soldier abundance ranges from 1 (scarce) to 4 (abundant). Values in brackets following species are estimated numbers of colonies sampled.

finely comminuted forage) but also eats the decayed surfaces of woody litter and logs, under the protective cover of soil-sheeting (Gay & Calaby 1970, M A-T personal observations). I was unable to locate published reference to chemical defence in *A. neogermanus*. Unlike *Amitermes* conspecifics which are lightly defended, *A. neogermanus* has evolved heavier defences

and exploits the (presumptive) high-risk harvesting niche. The above species have no nasus, hence soldiers need to make physical contact with the predator to transmit the secretion (Deligne 1971). The only available information on the proportion of soldiers in populations of such species in the wheatbelt comes from unpublished observations by H.

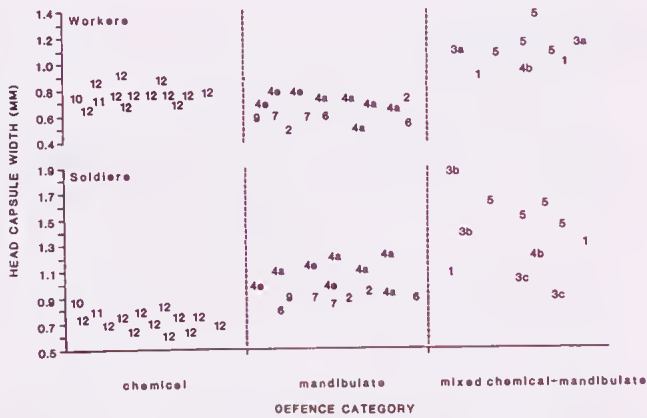


Figure 1. Soldier and worker head-capsule widths (as a measure of body size) of 38 termite species from the Western Australian wheatbelt. Species are categorized by their cephalic defence capabilities: mandibulate, chemical, mixed chemical-mandibulate (see Table 1). Measurements were carried out on the authors' reference material (mean of measurements on five specimens for each species). 1 *Coptotermes* sp.; 2 *Heterotermes* sp.; 3A *Schedorhinotermes* sp.; 3B *Schedorhinotermes* sp. major soldiers, 3C *Schedorhinotermes* sp. minor soldiers; 4A *Amitermes* sp. (excl. *A. neogermanus*); 4B *Amitermes neogermanus*; 5 *Drepanotermes* sp.; 6 *Ephelotermes argutus*; 7 *Microcerotermes* sp.; 8 *Paracaprithermes kraepelinii*; 9 *Xylochomitermes occidialis*; 10 *Nasutitermes exitiosus*; 11 *Occasitermes occasus*; 12 *Tumulitermes* sp.

Park (personal communication). His mound excavations of *Drepanotermes tammiuensis* colonies indicate that colony populations have ~ 16 % soldiers, which is comparable to figures reported for nasute species (Moore 1969, Haverty 1977).

The relationship between high-risk foraging, as in harvesting termites, and the need for an effective mechanism of defence, is best demonstrated with reference to the endemic *Drepanotermes* species, which have evolved within Australia from the predominantly wood-eating, almost cosmopolitan, smaller-bodied *Amitermes* (Watson & Perry 1981; Watson 1982; Watson & Gay 1991). Unfortunately, nothing is known about the appearance of the species from which it originally evolved. However, considering extant species of *Amitermes*, it appears that, in order to fill the large harvester niche in arid and semi-arid Australia, *Drepanotermes* has evolved large size in both workers and soldiers (Fig 1), and an abundant soldier caste (Table 1), displaying not only prominent mandibles but also an effective chemical defence (Moore 1969, Abensperg-Traun *et al.* 1991). *Amitermes neogermanus* shows similar adaptations.

Wood-eaters

Unlike harvesters, the large majority of wood-eating termites that rely on mandibulate defences, like those discussed here, live entirely within subterranean galleries and chambers, or within surface wood and thus rarely if ever venture into the open (Wood & Johnson 1986). Given that their interaction with surface predators such as ants and lizards is likely to be lower than that of the harvester species, their need for heavy soldier defence is also likely to be lower. This prediction is supported by the data because the majority of non-harvesters were lightly defended.

Moore (1969) reported the soldier caste of many Australian *Amitermes* species to represent < 0.1 % of total colony individuals (as against ~ 15 % for nasutitermitids and *Drepanotermes*). Many of their subterranean chambers contain a narrow entrance / exit at either or both ends (Fig 2F). In the case of a gallery breach, a single soldier, poking its prominent mandibles through the narrowed space, can effectively prevent the advance of ants. Mandibles of *E. argutus*, *P. kraepelinii* and *X. occidialis* can also be locked in a crossed position. The shield-like structure on the front of the head-capsule of soldiers assists in blocking chamber constrictions (Fig 2C), a habit known as phragmosis, which is seen most prominently in the wood-inhabiting *Kalotermitidae* (e.g. *Cryptotermes*; Gay & Watson 1982). However, harvester termites also incorporated such constricted spaces into their gallery and chamber systems (e.g. *Drepanotermes*, *A. neogermanus*). In the case of *A. obeuntis*, which has few soldiers (Table 1), the protective efficiency of its hard mound may have rendered the soldier caste largely redundant. The species is also known to frequently co-habit with *D. tamminensis* whose mounds are well defended by virtue of its hard surface and the abundant soldiers it contains (Abensperg-Traun 1988).

The relationship between predation risk and defence is taken to its extreme manifestation in the soldierless termites (Sands 1972). The absence of the soldier caste frequently occurs in soil-eating termites (Mill 1982); I interpret this to reflect their infrequent interaction with predatory ants, lizards and small mammals. Miller (1984, 1991) lists the northern

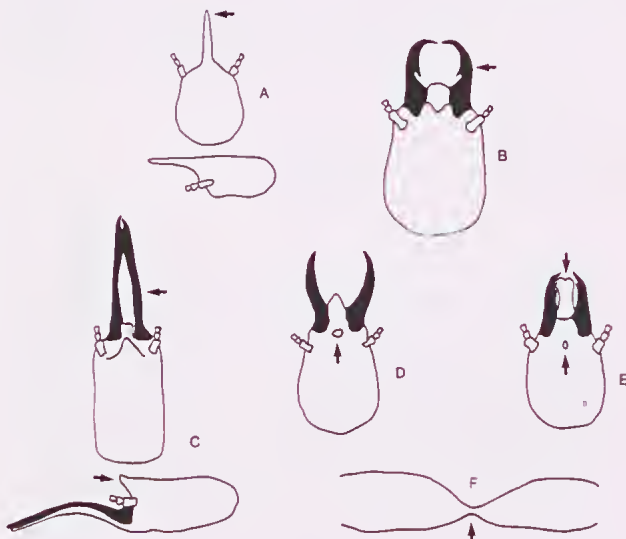


Figure 2. Defence mechanisms in termites from the Western Australian wheatbelt.

A *Tumulitermes petilus* (chemical); B *Amitermes obeuntis* (mandibulate); C *Ephelotermes argutus* (mandibulate); D *Coptotermes acinaciformis* (chemical-mandibulate); E *Schedorhinotermes reticulatus* (chemical-mandibulate); F termite chamber constriction. Arrows in D and E indicate the position of the fontanelle from which chemicals are secreted in *Coptotermes* and *Schedorhinotermes*, and applied via the labrum in *Schedorhinotermes* (E). Head-capsules were redrawn from Hill (1942) and Miller (1991). Drawings are not to scale.

Australian *Invasitermes mermis* and *I. insitivus* as soil-eating and soldierless. Possibly reflecting their lack of soldier defence but some pressure from predation, their colonies are frequently housed in the protective mounds of *Amitermes laurensis*. In revising the Australian *Termes*-*Capritermes* branch of the Termitinae, Miller (1991), lists several genera as humus and soil-eating, although these do not entirely lack a soldier caste (see also Watson & Gay 1991). However, soil-eating is restricted to high moisture habitats in humid forests and savannas (Wood *et al.* 1982), and is thus unlikely to be an important foraging strategy in the dry and infertile soils of the semi-arid wheatbelt. All known species of the revised *Termes*-*Capritermes* complex (*E. argutus*, *P. kraepelini*, *X. occidualis*), were eating wood in advanced stages of decay.

The presence of a frontal gland, and a pore (fontanelle) on the forehead for secretion of a chemical, is typical for both the Rhinotermitidae and the Termitidae (Watson & Gay 1991). Moore (1969) detected traces of chemical secretions in a small number of *Amitermes* sp. (e.g. *A. laurensis*) where soldiers are few and mandibulate. I have made similar observations involving three species of *Amitermes*. However, the scarcity of soldiers in such species is likely to make chemical soldier defence largely ineffective (Moore 1969).

There were six exceptions to the predicted relationship between wood-eating and low soldier defence. Consistent with all nasutid termites, the wood-eating *O. occasus* and *N. exitiosus* were defended by large numbers of small chemical soldiers. Such a defence appears appropriate in colonies of *N. exitiosus* which are housed in soft and thus easily breached mounds, readily exposing the colony to vertebrate predators such as echidnas which do, in fact, avoid mound-inhabiting *N. exitiosus* in the wheatbelt (Abensperg-Traun 1988). Wilson (1971) suggests that the optimal proportion of termite soldiers has evolved through selection to maximize (at minimal cost) the production of virgin males and females, as well as adequate defence of the colony. In that light, it seems odd that *O. occasus* retains what appears to be an unnecessarily large soldier caste which is expensive to maintain because soldiers need to be fed by the workers.

Consistent with other rhinotermitids, soldiers of *Schedorhinotermes* and *Coptotermes* were moderately abundant (Table 1) with chemical defence capabilities, in addition to prominent mandibles (Quennedey & Deligne 1975; Blum *et al.* 1982). The clear secretions of *Schedorhinotermes* sp. soldiers are applied by means of an extended labrum, or "daubing brush" (Fig 2E), whereas *Coptotermes* soldiers emit a milky latex from a fontanelle when disturbed (Fig 2D). Although I was unable to detect secretions in *Schedorhinotermes* sp. soldiers, chemical defence in this taxon is well known and documented (Quennedey 1975). *Heterotermes* species also have a small fontanelle, but it is not known whether this is functional.

Future Research

Whereas the general study predictions were upheld by the data, differences in predation levels between harvesters and non-harvesters remain to be substantiated. Although the scarcity of soldiers among most wood-eaters may have alternative explanations, the most plausible explanation is a low risk foraging environment. Clearly, much remains to be discovered not only about the foraging behaviour of particular

species, especially the rarer ones which comprise the majority (Abensperg-Traun & De Boer 1990; Abensperg-Traun 1991), but also about the evolutionary forces that may have shaped the morphological and chemical adaptations seen in termites today (Hare 1937). For instance, with an increase in food quality (C:N ratio), the fecundity of termite colonies may also increase (Waller & La Fage 1987). With high fecundity, heavy investment in colony defence (e.g. a high soldier:worker ratio) to compensate for predation losses may be unnecessary. Whether relatively fecund termites (possibly those inhabiting nutrient-rich environments) are less heavily defended than less fecund species (possibly those inhabiting nutrient-poor environments) is poorly known and would provide interesting research.

There are other aspects that need to be considered when discussing interactions between termite foraging strategies and their mechanisms of defence, but relevant observations are lacking. For instance, the proportion of soldiers within colonies may vary significantly with season and age of the colony (Bouillon 1969), and this may relate in some way to foraging requirements. The size of the cephalic gland, and the chemical composition of secretions often differs between genera and even between congeneric species (Bouillon 1969, Prestwich 1979, Blum *et al.* 1982). Some species possess a dimorphic soldier caste, with major and minor forms that differ significantly in size (e.g. *Schedorhinotermes* sp.; Fig 1). How these factors complement each other in defence of foraging parties remains poorly understood.

The wider question of the effects of predation on termite populations, partially related to foraging strategy and the efficiency of defence mechanisms, is poorly understood. In Nigerian savanna, for instance, annual predation on *Macrotermes* sp. by one species of ant alone is 2.7-fold the standing crop of workers and soldiers (Longhurst *et al.* 1978). Although no Australian ants are known to be termite-specialists (A N Andersen and S Higashi, personal communications), species of *Iridomyrmex* ants in particular appear to be important termite predators (Greenslade 1970, Higashi & Ito 1989, Holt 1990). Given the significant ecological role attributed to termites, particularly in tropical and subtropical Australia (Stafford Smith & Morton 1990) where termites may compete with livestock for food (Watson *et al.* 1973), a detailed investigation into the effects of predation on termite populations is likely to be rewarding. The question that may be posed is whether termite populations are limited by predation, or other factors such as food and competition.

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References

- Abensperg-Traun M 1988 Food preference of the echidna, *Tachyglossus aculeatus* (Monotremata: Tachyglossidae), in the wheatbelt of Western Australia. *Australian Mammalogy* 11:117-123.
- Abensperg-Traun M 1990 Patch Selection and Patch Use in the Echidna, *Tachyglossus aculeatus* Shaw 1792 (Monotremata: Tachyglossidae), in Western Australian Wheatbelt Reserves. PhD thesis, University of Western Australia.
- Abensperg-Traun M 1991 Seasonal changes in activity of subterranean termite species (Isoptera) in Western Australian wheatbelt habitats. *Australian Journal of Ecology* 16:331-336.
- Abensperg-Traun M & De Boer E S 1990 Species abundance and habitat differences in biomass of subterranean termites (Isoptera) in the wheatbelt of Western Australia. *Australian Journal of Ecology* 15:219-226.

- Abensperg-Traun M, Dickman C R & De Boer E S 1991 Patch use and prey defence in a mammalian myrmecophage, the echidna (*Tachyglossus aculeatus*) (Monotremata: Tachyglossidae): a test of foraging efficiency in captive and free-ranging animals. *Journal of Zoology* (London) 225:481-493.
- Blum M W, Jones T H, Howard D F & Overal W L 1982 Biochemistry of termite defenses: *Coptotermes*, *Rhinotermes* and *Cornitermes* species. *Comparative Biochemistry and Physiology* 71B:731-733.
- Bouillon A 1969 Termites of the Ethiopian Region. In: *Biology of Termites*, vol. 2 (ed K Krishna & F M Weesner) Academic Press, New York, 154-280.
- Coles de Negret H R & Howse P E 1983 Chemical defence in termites - ecological aspects. In: *Social Insects in the Tropics* (ed P Jaisson) Universite Paris-Nord, Paris, 21-29.
- Deligne J 1965 Morphologie et fonctionnement des mandibules chez les soldats des termites. *Biologica Gabon* 1: 179-186.
- Deligne J 1971 Mechanics of the fighting behaviour of the termite soldiers (Insecta: Isoptera). *Forma Functio* 4: 176-187.
- Eisner T E, Kriston I & Aneshansley D J 1976 Defensive behaviour of a termite (*Nasutitermes exitiosus*). *Behavioural Ecology and Sociobiology* 1:83-125.
- Gay F J & Calaby J H 1970 Termites of the Australian region. In: *Biology of Termites* (ed K Krishna & F M Weesner) Academic Press, New York, 393-448.
- Gay F J & Watson J A L 1982 The genus *Cryptotermes* in Australia (Isoptera: Kalotermitidae). *Australian Journal of Zoology, Supplementary Series* No. 88:1-64.
- Greenslade P J M 1970 Observations on the inland variety (v. *viridiaeneus* Niehmeyer) of the meat ant *Iridomyrmex purpureus* (Frederick Smith) (Hymenoptera: Formicidae). *Journal of the Australian Entomological Society* 9:227-231.
- Hare L 1937 Termite phylogeny as evidenced by soldier mandible development. *Annals of the Entomological Society of America* 30:459-486.
- Haverty M I 1977 The proportion of soldiers in termite colonies: a list and a bibliography. *Sociobiology* 2:199-216.
- Higashi S & Ito F 1989 Defence of termitaria by termitophilous ants. *Oecologia* 80:145-147.
- Hill G F 1942 Termites (Isoptera) from the Australian Region. CSIRO, Melbourne.
- Holt J A 1990 Observations on the relationship between meat ants and termites in tropical Australia. *Journal of Tropical Ecology* 6:379-382.
- Longhurst C, Johnson R A & Wood T G 1978 Predation by *Megaponera foetens* (Fabr.) (Hymenoptera: Formicidae) on termites in the Nigerian southern Guinea savanna. *Oecologia* 32:101-107.
- McMahan E A 1974 Non-aggressive behaviour in the large soldier of *Nasutitermes exitiosus* (Hill) (Isoptera: Termitidae). *Insectes Sociaux* 21:95-106.
- Mill A E 1982 Foraging and Defensive Behaviour in Neotropical Termites. PhD thesis, University of Southampton.
- Miller L R 1984 *Invasitermes*, a new genus of soldierless termites from northern Australia (Isoptera: Termitidae). *Journal of the Australian Entomological Society* 23:33-37.
- Miller L R 1991 A revision of the *Termes-Capititermes* branch of the Termitinae in Australia (Isoptera: Termitidae). *Invertebrate Taxonomy* 4:1147-1282.
- Moore B P 1969 Biochemical studies in termites. In: *Biology of Termites*, vol. 1 (ed K Krishna & F M Weesner) Academic Press, New York, 407-432.
- Prestwich G D 1979 Interspecific variation in the defence secretions of *Nasutitermes* soldiers. *Biochemical Systematics and Ecology* 7:211-221.
- Prestwich G D 1988 The chemicals of termite societies (Isoptera). *Sociobiology* 14:175-191.
- Quennedey A 1975 The labrum of *Schedorhinotermes minor* soldier: morphology, innervation, and fine structure. *Cell Tissue Research* 160: 81-98.
- Quennedey A & Deligne J 1975 L'arme frontale des soldats de termites. I. *Rhinotermitidae*. *Insectes Sociaux* 22:243-267.
- Richardson P R K 1987 Aardwolf: the most specialized myrmecophagous mammal? *South African Journal of Science* 83:643-646.
- Sands W A 1972 The soldierless termites of Africa (Isoptera: Termitidae). *Bulletin of the British Museum of Natural History (Entomology)* Supplement No 18:1-244.
- Skaife S H 1955 *Dwellers in Darkness*. Longmans, New York.
- Stafford Smith D M & Morton S R 1990 A framework for the ecology of arid Australia. *Journal of Arid Environments* 18:255-278.
- Waller D A & La Fage J P 1987 Nutritional ecology of termites. In: *Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates* (ed F Slansky Jr & J G Rodriguez) Wiley & Sons, New York, 487-532.
- Watson J A L 1982 Distribution, biology and speciation in the Australian harvester termites, *Drepanotermes* (Isoptera: Termitinae). In: *Evolution of the Flora and Fauna of Arid Australia* (ed W R Barker & P J M Greenslade) Peacock Publications, Adelaide, 263-265.
- Watson J A L & Gay F J 1991 Isoptera. In: *The Insects of Australia*, 2nd ed, vol 1 (ed Division of Entomology, CSIRO) Melbourne University Press, Melbourne, 330-347.
- Watson J A L, Lendon C & Low B S 1973 Termites in mulga lands. *Tropical Grasslands* 7:121-126.
- Watson J A L & Perry D H 1981 The Australian harvester termites of the genus *Drepanotermes* (Isoptera: Termitinae). *Australian Journal of Zoology* Supplement Series No 78:1-153.
- Wilson E O 1971 *The Insect Societies*. Belknap Press of Harvard University, Cambridge.
- Wood T G 1978 Food and feeding habits of termites. In: *Production Ecology of Ants and Termites* (ed M V Brian) Cambridge University Press, Cambridge, 55-80.
- Wood T G & Johnson R A 1986 The biology, physiology, and ecology of termites. In: *Economic Impact and Control of Social Insects* (ed S B Vinson) Praeger, USA, 1-68.
- Wood T G, Johnson R A, Bacchus S, Shittu M O & Anderson J M 1982 Abundance and distribution of termites (Isoptera) in a riparian forest in the southern Guinea savanna vegetation zone of Nigeria. *Biotropica* 14:25-39.

Typology, Petrology, and Palynology of the Broke Inlet Biface, a Large Flaked Chert Artifact from South-western Australia

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Abstract

The Broke Inlet biface is the largest chert artifact (1797 g) recovered from any prehistoric site in south-western Western Australia. It is an incompletely flaked core taken from shallow water at Broke Inlet, an estuary on the southern coast. Its large size has allowed the preservation of minerals, fossils and textures that are normally destroyed in smaller chert objects such as flakes by weathering or ground-water solution. This makes it a suitable frame of reference for the description of other chert artifacts from the south-west of Western Australia. The chert was formed by silicification of a foraminiferal and bryozoal late Middle or Late Eocene limestone containing apparent sponge spicules and minor pyrite, glauconite, and apparent argillaceous matter. Silicification probably took place shortly after deposition, *i.e.* within the Eocene. On acid digestion, the biface yielded abundant dinoflagellates but no spores or pollen. The dinoflagellate assemblage differs significantly from that in the Dunsborough implement and the Kings Park Formation, and has strong affinities with assemblages from units in the Otway and St. Vincent Basins of south-eastern Australia. The limestone protolith of the chert was probably deposited in water 50-100m deep, in the Eocene sea separating Australia and Antarctica. All evidence indicates that the Plantagenet Group is the provenance of the biface.

Introduction

One of the rocks widely used as raw material for artifacts in south-western Western Australia (see Fig 1) is secondary Eocene chert. There are three significant dates in the history of all such artifacts: the date of sedimentation of the precursor of the chert (the protolith), the date of silicification, and the

date of quarrying. Palaeontology (including palynology) can give the first date, and may throw light on the environment of deposition. The time of silicification is more difficult to determine, and can generally only be positioned relative to other events in the diagenetic sequence. However, the world-wide selective silicification of Eocene strata suggests that the silicification was an Eocene process (Gartner 1970): according to McGowran (1989) it reached its peak in the early Middle Eocene. In other words, silicification probably took place during the same geological epoch, and perhaps within the same geological age, as deposition. Quarrying and fashioning of the artifacts was a feature of the prehistoric human occupation of Australia, *i.e.* of the upper Quaternary. Local occupation has been shown to date back 30,000-40,000 years BP (Pearce & Barbetti 1981, Dortch 1984) and may extend further.

In south-western Western Australia, the Eocene protoliths of the chert were being deposited in two dissimilar marine environments: the open, generally warm-water area of the eastern Indian Ocean, and the more restricted, probably cooler waters of the widening channel of the southern ocean that had spread between Australia and Antarctica. These chert provenances have been informally labelled the western and south-eastern provenances (Glover 1979). The distribution of exposed strata of the Eocene Plantagenet Group is shown in Hocking (1990).

Eocene chert artifacts on the surface of the Perth Basin and Leeuwin Complex, and the western margin of the Yilgarn Craton, are believed to come from now-submerged formations in the western provenance which were exposed and quarried when sea-level was lower (see Fig 1). Eocene

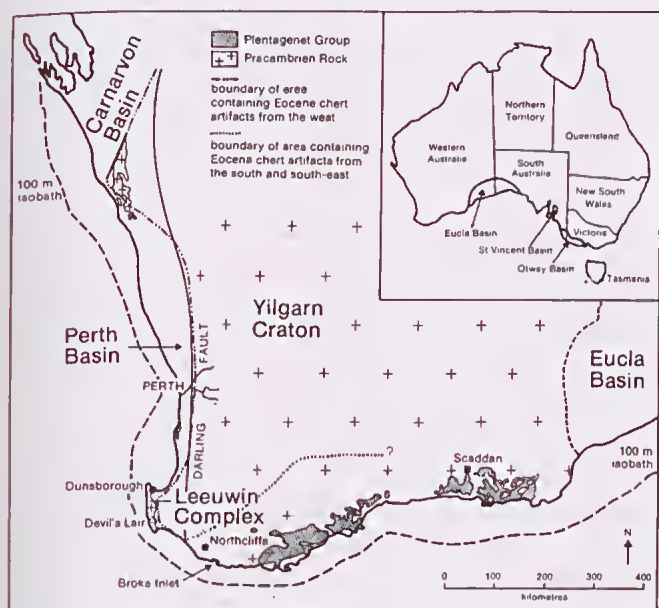


Figure 1. Map showing places referred to in the text.

chert artifacts are also found east of the Darling Fault along the southern coast and in its hinterland. Some of the chert from this region is petrologically indistinguishable from the western chert but some contains colloform opal, which is absent from chert found in the west. The opal-bearing chert probably came from the south-eastern provenance comprising onshore Plantagenet Group rocks, and rocks farther south that are now submerged: the accompanying non-opalline chert may have come from the same general area, or possibly from the west. There are many gaps in our knowledge of the geoarchaeology of this provenance.

Some general considerations apply to the study of artifacts from south-western Australia. Palynological assemblages within small artifacts such as flakes are destroyed by weathering, or by percolating solutions, depending on the environment, but they can survive in larger objects such as bifaces. Pyrite and carbonaceous matter persist well in the larger objects, but are destroyed in flakes. Calcite and glauconite are found in some flakes, but have probably been destroyed in many. It follows that studies of the petrology and palynology of large bifaces can make the best contribution to our understanding of the geology of local chert artifacts.

The depositional age of flakes from the western provenance has been indicated from foraminifera and bryozoa (Glover & Cockbain 1971, Quilty 1978), and may be Middle or Late Eocene. The geological age of the Dunsborough implement (also from the western provenance) was shown by pollen (Glover *et al.* 1978) to be Early or Middle Eocene. The typology and archaeological provenance, petrology, and palynology of the Broke Inlet biface are described below, so that it can be fitted into the temporal framework outlined above.

Archaeological Provenance and Typology of the Broke Inlet Biface

The large chert biface illustrated in Fig 2 was collected by one of us (CED) in shallow water at Broke Inlet, one of the major estuaries along the southern coast of south-western Australia (Fig 1). The find site of this and 24 other Aboriginal stone artifacts and manuports (*i.e.* unmodified stones brought from elsewhere) is near the north-east end of the estuary, about 400m from the north shore. The artifacts were 50 cm underwater on the flat estuary floor, consisting here of unconsolidated white sand, interspersed with patches of dark brown cemented sand. This latter unit appears to be the hardpan of a humus podzol, which is the soil type on the poorly drained sand plain of the estuary's landward margins (Churchward *et al.* 1988: 12, Northcliffe and Deep River-Nornalup Landform and Soil Maps). Very occasional blackboy stumps (*Xanthorrhoea preissii*) are present in growth position in the dark brown cemented sand, which probably pre-dates the estuary's formation at the end of the Flandrian transgression, c. 6000 yr BP (Hodgkin & Clark 1989, p.3). Most of the artifacts were lying on the white sand, on what may be a thin lens overlying the cemented sand; others were lying directly on the latter unit, though none was *in situ* in it. It is nevertheless possible that all or some of the artifacts derive from the cemented sand, or from the missing upper horizons of the original soil of which it was presumably part. On the other hand, the assemblage may be largely or entirely attributable to human activities on the estuary floor during times of low water level. Broke Inlet, which is normally a

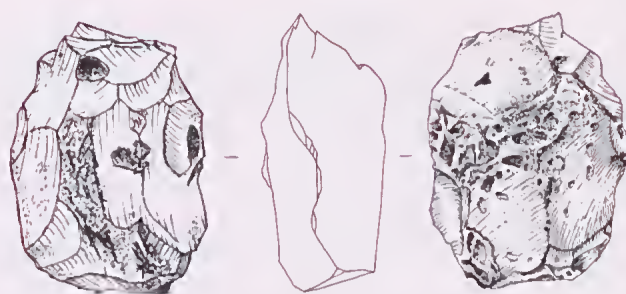


Figure 2. Sketch of Broke Inlet biface.

waterbody covering 48 km², partially dries up during periods of major drought, with its deepest parts remaining as shallow pools surrounded by sand flats.

The artifacts from this site are registered in the Anthropology collection of the Western Australian Museum under the numbers B3879 (the biface and a chert flake) and B3900 (23 other specimens, including quartzite flakes and fragments, pebbles and a percussion/grindstone). The site is numbered S2594 in the registry of the Western Australian Department of Aboriginal Sites. Its geographic position is 34° 56' 15"S, 116° 30' 00"E.

Typological Description

The absence of use-wear or other damage suggestive of use on its edges shows that the Broke Inlet biface is probably not an implement or a tool, but a large core, flaked by direct percussion with a hammerstone to obtain large flakes for use as scraping or cutting tools. The piece is a biface, a category that includes both tools and cores. It is of generalised form, and flaked alternately on its opposing faces. Flake scar facets indicate at least nine major flake removals on its right hand face (see Fig 2), and another six or more flake removals on the opposing face. Unlike the many "exhausted" cores found in archaeological sites, it seems to have been discarded or lost by its knapper at a stage when more large flakes could have been removed from part of both faces. None of the flakes removed from this biface was present in the assemblage, and the only large chert flake collected is of a different petrological facies (see below).

Maximum length of the Broke Inlet biface is 181 mm: its weight is 1797 grams. This is the largest chert artifact known to us from any prehistoric site in the south-west of Western Australia. The original unflaked mass must have been a good deal greater than that of the present biface, which was reduced in size by the removal of large flakes, as shown by the large negative flake scars on parts of both faces, especially some of those in the left-hand view in Fig 2. The larger of these flake scars was struck from a former striking platform which would have been to the right of the right-hand side of the biface, as shown in this view. The weight of the original nodule could easily have been over 3-4 kg. Even if the original nodule had been flaked at its source, the present biface weighing 1797 g would still seem too large to have been carried many km from its place of origin, which may have been either a chert outcrop, or a fluvial or marine deposit incorporating nodules, cherty horizons, or chert clasts.

Archaeological Implications

The Broke Inlet biface is one of several bifacially flaked chert artifacts collected in south-western Australia, and named after their find sites. One of these, known since the 1940's as the Scaddan implement, is considered to be anomalous, and is almost certainly an Acheulian (Lower Palaeolithic) hand axe, judging by its technique, style, surface patination, stone texture, colour and rolled condition. The Scaddan implement analysis concluded that the piece was probably brought from England earlier this century, though a European origin could not be verified by means of petrological and palaeontological examination of its constituent stone (Dortch & Glover 1983).

A second biface, named the Dunsborough implement, was shown to be of Australian origin. Typologically the Broke Inlet biface and the Dunsborough implement are very similar, and the latter is also probably a core, even though it is very much smaller, weighing only 300 g, with a maximum length of 106 mm. The few other bifacially flaked cores made of Eocene chert that have been found at prehistoric sites in south-western Australia are even smaller. Most are discoidal in form and much more delicately flaked than the Broke Inlet and Dunsborough specimens. One Eocene chert biface from the Ellen Brook site *ca* 20 km south of Dunsborough (Fig 1) seems to be a tool rather than a core (Dortch & Glover 1983, Fig 5).

Neither the Broke Inlet biface nor the Dunsborough implement was found in an archaeologically datable context. However, because quarries in Eocene chert were probably inundated by rising seas before about 6000 BP (see Glover 1984), each is likely to be late Pleistocene or Early Holocene in age.

Petrology

Handspecimen

For geological purposes a solid cylindroidal core 4x2.5 cm was drilled into the underside of the specimen: part of it was used for thin-sectioning, and the remainder for the extraction of palynomorphs. The top of the core was retained so that the biface could be restored to its original appearance.

The surface of the specimen where drilled ranges in colour from dark grey (N3) through brownish grey (5YR4/1) and light brown (5YR5/6) to locally very pale orange (10YR8/2) (colours according to Rock-Color Committee, Geological Society of America, 1963). For about 1.5 cm below the surface, the rock is very light grey (N8) changing downward to pinkish grey (5YR8/1) before passing into apparently fresh rock that is irregularly coloured from light grey (N7) to medium grey (N5). In the fresh rock there are three thin (<2mm thick) discontinuous irregular horizons that are locally dark grey (N3). Colour bands are roughly parallel to the extension of the specimen, which in turn is roughly parallel to bedding. Foraminifera and Bryozoa are visible under the hand lens and to the naked eye: where elongate, they are parallel to bedding. Effervescence in dilute HCl is limited to isolated spots.

Thin Section

Under the microscope, the rock can be seen to be a chert made up mainly of a grey opalline matrix, probably with argillaceous impurity, which contains abundant silicified bryozoal, foraminiferal, and other originally calcareous detritus (Fig 3). There are also numerous vaguely defined elongate grains up to about 0.5mm long that are probably sponge spicules.

Foraminiferal shell walls are well defined: they consist mainly of fine-grained quartz or chalcedony. Some chambers are filled or partly filled with grey opal, but most are filled with coarse chalcedony. Less commonly, chambers are filled with a brown isotropic mineral resembling opal, but of uncertain composition: the material may consist of matrix that has been only partly silicified. The inner walls of fossil chambers containing chalcedony are commonly outlined by a fringe of roughly wedge-shaped objects, commonly about 0.01mm long, with pronounced negative relief that causes them to appear dark grey to black under low magnification. The objects are rare in chambers filled with opal, and they



Figure 3. Photomicrograph of chert from Broke Inlet biface showing cross-section of bryozoan (mainly white) set in a grey matrix of impure, probably argillaceous opal. The walls of the bryozoan are composed of fine chalcedony (white), and the chambers are filled with coarser chalcedony (white) and opal (grey). Note the well-defined fringe of dark, wedge-shaped cavities on the chamber walls. The light-coloured objects in the grey matrix are fossil debris, mainly spicules, and the dark patches contain limonite. Plane-polarised light. Width of field 1.35 mm.

make up <1% of the rock. Examination under the scanning electron microscope reveals that the objects are cavities. Other material which makes up <5% of the rock includes minute dark fragments that are probably carbonaceous, pyrite framboids that are brassy in reflected light, green grains showing the aggregate polarisation typical of glauconite, and small isolated patches of calcite. Close to the artifact surface there are pale brown spots of limonite.

Petrological interpretation

The chert is a silicified impure limestone in which the forms of silica reflect most of the original fabric. Quartz and chalcedony replace shell walls, impure opal substitutes for

the argillaceous and calcareous matrix, and chalcedony occupies chambers that may have been largely empty before silicification. As usual in Western Australian secondary Eocene chert, glauconite has not been altered to silica. The framboids of pyrite described here are absent from chert flakes, because the smaller size of the flakes allows the penetration of oxidising fluids.

The minute, inwardly directed wedge-shaped cavities forming dark inner fringes to many of the chambers are common in Western Australian artifacts of Eocene chert and have been noted in previous petrological descriptions (Glover 1975, Glover *et al.* 1978). The cavities probably formed by the dissolution of a fringe of crystals (perhaps carbonate) growing into the centre of the chambers from the walls. If so, the mineral apparently never filled the cavities, because the successful crystals would have increased in diameter inwardly, to give the classic drusy carbonate fabric. The chalcedonic filling, on the other hand, has an irregular texture, and may have been formed from silica gel that filled the remaining space. A hypothetical diagenetic sequence that would account for the observed texture is as follows: a fringe or lining of calcite grows on the inner surface of the shell, and is followed by silica gel which fills the remaining space and converts to chalcedony and quartz, after which the calcite forming the fringe dissolves. Probably at about the same time, clay-carbonate matrix is converted to impure opal, and shells are silicified.

The palimpsest (ghost) fabric allows reconstruction of the original rock as a fossiliferous, impure limestone or, more precisely, a foraminiferal, bryozoal, and spicular lime wackestone containing minor glauconite, pyrite, and carbonaceous material, and probably clay minerals (classification of Dunham 1962).

Foraminiferal Palaeontology

Foraminifera are best studied after extraction from sedimentary rock, a process not possible with chert. The silicified foraminifera observed here in thin section consist of smaller benthonic rotaliids and very small planktonic forms. The foraminifers *Subbotina*, a very small spinose *Acarinina*, and possible primitive *Turborotalia cerroazulensis* suggest middle Eocene age (D W Haig, pers. comm.). The biota indicate a mid-neritic (50-100m) depth of deposition for the limestone.

Palynology

The dinoflagellate assemblage

Two separate extractions of acid-insoluble organic matter were undertaken from chips of the artifact to provide adequate material for palynological analysis. The extracts are small but similar in composition, indicating that they indeed represent *in situ* assemblages with no laboratory contamination.

The organic extract consists primarily of dinoflagellates (marine microplankton) and sapropel, with lesser amounts of carbonaceous material. Not a single spore or pollen was observed, and plant cuticular material was rare. This is

evidence of a marine depositional environment with negligible terrestrial input. The following dinoflagellate species, several of them undescribed, were identified. Some key forms are illustrated in Figure 4.

Aireiana verrucosa Cookson & Eisenack 1965 - Figure 4 J,K

Batiacasphaera sp.

Circulodinium? sp. - Figure 4 A,B

Cleistosphaeridium spp.

Cordosphaeridium inodes (Klumpp 1953) Eisenack 1963

Cordosphaeridium sp.

Corrudinium incompositum (Drugg 1970) Stover & Evitt 1978 - Figure 4 L,M

Deflandrea sp.

Fibrocysta sp. - Figure 4 H,I

Gen. et sp. indet. - Figure 4 G

Homotryblum floripes (Deflandre & Cookson 1955) Stover 1975 - Figure 4 D

Impagidinium victorianum (Cookson & Eisenack 1965) Stover & Evitt 1978 - Figure 4 E,F

Operculodinium centrocarpum (Deflandre & Cookson 1955) Wall 1967

Operculodinium sp.

Spiniferites spp.

Systematophora placacantha (Deflandre & Cookson 1955) Davey *et al.* 1969

cf. *Systematophora* sp.

Tectatodinium pellitum Wall 1967 - Figure 4 C

Fibrocysta sp. and *Tectatodinium pellitum* are common in the sample, with *Circulodinium*? sp. and *Homotryblum floripes* next in abundance.

Provenance, age, and correlation

The presence in the sample of *Aireiana verrucosa*, whose only previously published records are from south-eastern Australia, is consistent with the sample being of Australian rather than of foreign origin. *A. verrucosa* has been recorded from the Otway Basin in Victoria (Cookson & Eisenack 1965, Stover 1975) and the St. Vincent Basin in South Australia (Harris 1985).

The age of the chert dinoflagellate assemblage can be addressed by correlation with Eocene dinoflagellate assemblage zones erected for south-eastern Australia by Harris (1985). This zonation built on earlier work by Partridge (1976) and can be compared with the New Zealand zonation of Wilson (1984, 1985).

The chert dinoflagellate assemblage correlates unequivocally with the *Corrudinium incompositum* zone of Harris (1985). That zone is dated by correlation with the planktonic foraminiferal zones proposed by Berggren (1969) and the spore-pollen zonations of Harris (1971) and Stover & Partridge (1973) as latest Middle to Late Eocene (Harris 1985). Marshall and Partridge (1988, p.242 and fig 4) imply that the *C. incompositum* zone is entirely Late Eocene in age.

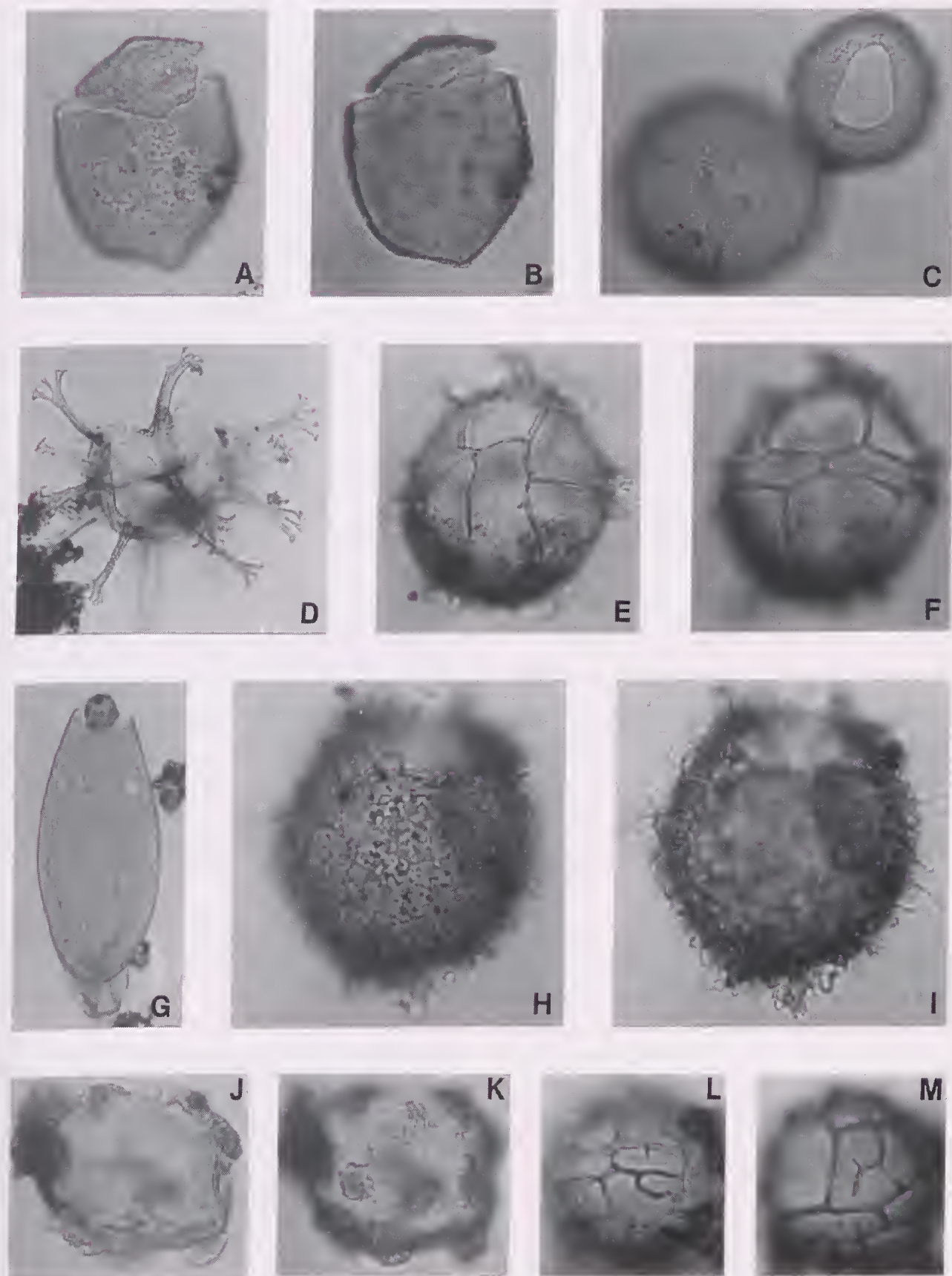


Figure 4. Dinoflagellates from the Broke Inlet biface; all magnified X500 except L,M X1000. A,B, *Circulodinium?* sp., ventral view, high and intermediate focus; C, *Tectatodinium pellitum*, two specimens; D, *Homotryblum floripes*; E,F, *Impagidinium victorianum*, ventral view, high and low focus; G, Gen. et sp. indet.; H,I, *Fibrocysta* sp., dorsal view, high and intermediate focus; J,K *Aireiana verrucosa*, high and low focus; L,M, *Corrudinium incompositum*, right lateral view, high and low focus.

Zonal indicators extracted from the chert include *Corrudinium incompositum*, which typifies the zone, and *Aireiana verrucosa*, which makes its first stratigraphic appearance in the zone, and is restricted to the Late Eocene. *C. incompositum* was first described from the Oligocene of the Gulf Coast, U.S.A. (Drugg 1970), but in Australia is restricted to the Late Eocene (and possibly the late Middle Eocene). It has been recorded from the Gippsland Basin (Marshall & Partridge, 1988), the Otway Basin (A D Partridge, pers. comm.), the St. Vincent Basin (Harris, 1985), and the eastern Eucla Basin (Benbow *et al.* 1982). *A. verrucosa* has been reported from the Otway Basin (Cookson & Eisenack 1965, Stover 1975), and the St. Vincent Basin (Harris 1985).

Other age-diagnostics species include *Tectatodinium pellitum*, *Homotryblium floripes*, *Systematophora placacantha* and *Impagidinium victorianum*. The first three species are widely occurring, with each having an oldest occurrence of Middle Eocene. *I. victorianum* has been reported from Middle to Late Eocene sediments offshore eastern Canada (Williams & Bujak 1977), but in Australia appears to be restricted to the Late Eocene. It has been reported from offshore Tasmania (Haskell & Wilson 1975), the Otway Basin (Cookson & Eisenack 1965) and the western Eucla Basin (Milne 1988).

In summary, a Late Eocene age is likely for the chert dinoflagellate assemblage, although a late Middle Eocene age cannot be entirely discounted.

The palynology of the Dunsborough implement from the Perth Basin was described by Glover *et al.* (1978). Dinoflagellates were extracted from that artifact but the assemblage has little in common with the one described here, and in addition spores and pollen were prominent. An Early to Middle Eocene age was suggested for the Dunsborough implement, and a strong similarity was noted with the microflora described by Cookson & Eisenack (1961) from the Kings Park Formation (this unit in the Rottnest Island Bore is now referred to the Porpoise Bay Formation: see Cockbain & Hocking 1989). The dinoflagellate assemblage described here is quite different from both those assemblages, and displays much stronger affinities with south-eastern Australian assemblages.

The Broke Inlet biface dinoflagellate assemblage is most similar to microfloras described from the Browns Creek Formation of the onshore Otway Basin (Cookson & Eisenack 1965, Stover 1975, A D Partridge pers. comm.) and the Tortachilla Limestone and Blanche Point Formation of the St. Vincent Basin (Harris 1985). These stratigraphic units are age equivalent to the Plantagenet Group in the Bremer Basin according to Harris (1985), and are part of his "Depositional Sequence 3" which is developed right across southern Australia. Thus the similarity between this chert assemblage, which is no doubt derived from the Plantagenet Group, and south-eastern Australian Late Eocene assemblages can be explained by their similar geological setting in relation to the opening Southern Ocean between Australia and Antarctica.

The palynology of the Werillup Formation of the Plantagenet Group has been addressed by Hos (1975) and Stover & Partridge (1982). Hos (1975) noted the presence of dinoflagellates in his material from near Albany but did not document the assemblage. Stover and Partridge (1982) reported that their material from the Fitzgerald River area to the east was nonmarine. In the light of the assemblage described here, future work is necessary to document the dinoflagellates of the Plantagenet Group.

Discussion

The chert artifacts of south-western Australia seem to come from various stratigraphic horizons ranging from Early to Late Eocene (Glover 1984), and are evidently products of the pronounced world-wide process of Eocene silicification, which according to McGowran (1989) reached its peak in the early Middle Eocene.

The Broke Inlet biface artifact has been derived from silicified foraminiferal and bryozoal fine-grained limestone or argillaceous limestone containing a little glauconite, which was similar to protoliths of chert used for the artifacts found along western and southern coastal areas generally. Distance from shore could have accounted for the absence of floral material and clastic mineral debris from the Broke Inlet biface: perhaps also winds were mainly onshore. The large weight of the biface suggests that it may not have been carried far from its place of quarrying.

The environment along the southern coast as Australia drifted northward from Antarctica was probably cooler and more restricted than that along the western coast facing the open Indian Ocean, and it may have affected the mineralogy, diagenesis and palaeontology in ways not yet appreciated. The reason for the abundance of opal in some southerly derived artifacts has not yet been accounted for. Nevertheless, the south-coastal position of the find at Broke Inlet, the implication of short transportation from the weight of the biface, the high opal content, and the palynological similarities to Eocene rocks from the St. Vincent and Otway Basins, combine to indicate derivation from sediments deposited in the Eocene marine channel separating Australia from Antarctica, rather than off the west coast of south-western Australia. The excellent preservation of many of the mineralogical, textural and micropalaeontological features will make the biface an object of useful comparison for other large chert artifacts from the south-west of Western Australia. Fortunately, it is possible with current techniques to extract material for analysis without permanently affecting the external appearance of the artifacts.

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References

- Benbow M C, Lindsay J M, Harris W K & Cooper B J 1982 Latest Eocene marine incursion, northeast margin of the Eucla Basin. Quarterly Geological Notes of the Geological Survey of South Australia 81:2-9.
- Berggren W A 1969 Cenozoic chronostratigraphy, planktonic foraminiferal zonation and the radiometric time scale. Nature 224:1072-1075.
- Churchward H M, McArthur W M, Sewell P L & Bartle G A 1988 Landforms and soils of the south coast and hinterland, Western Australia. CSIRO, Division of Water Resources, Divisional Report 88/1, Canberra.
- Cockbain A E & Hocking R M 1989 Revised stratigraphic nomenclature in Western Australian Phanerozoic basins. Western Australian Geological Survey, Record 1989/15.
- Cookson I C & Eisenack A 1961 Tertiary microplankton from the Rottnest Island Bore, Western Australia. Journal of the Royal Society of Western Australia 44:39-47.
- Cookson I C & Eisenack A 1965 Microplankton from the Browns Creek Clays, SW. Victoria. Proceedings of the Royal Society of Victoria 79:119-131.
- Dortch C E 1984 Devil's Lair, a Study in Prehistory. Western Australian Museum Press, Perth.

- Dortch C E & Glover J E 1983 The Scaddan implement, a re-analysis of a possible Acheulian handaxe found in Western Australia. *Records of the Western Australian Museum* 20: 318-334.
- Drugg W S 1970 Some new genera, species, and combinations of phytoplankton from the Lower Tertiary of the Gulf Coast, USA. *Proceedings of the North American Paleontological Convention, September 1969, Part G*, Allen Press, Lawrence, Kansas, 809-843.
- Dunham R J 1962 Classification of carbonate rocks according to depositional texture. In: *Classification of Carbonate Rocks* (ed W E Ham). American Association of Petroleum Geologists, Tulsa, 108-121.
- Gartner S 1970 Sea-floor spreading, carbonate dissolution level, and the nature of horizon A. *Science* 169:1077-1079.
- Glover J E 1975 The petrology and probable stratigraphic significance of Aboriginal artifacts from part of south-western Australia. *Journal of the Royal Society of Western Australia* 58:75-85.
- Glover J E 1979 The provenance and archaeological significance of Aboriginal artifacts of Eocene chert in southwestern Australia. *Search* 10:188-190.
- Glover J E 1984 The geological sources of stone for artifacts in the Perth Basin and nearby areas. *Australian Aboriginal Studies* 1984:17-25.
- Glover J E & Cockbain A E 1971 Transported Aboriginal artefact materials, Perth Basin, Western Australia. *Nature (London)* 234:545-546.
- Glover J E, Dortch C E & Balme B E 1978 The Dunsborough instrument: an Aboriginal biface from southwestern Australia. *Journal of the Royal Society of Western Australia* 60:41-47.
- Harris W K 1971 Tertiary stratigraphic palynology, Otway Basin. In: *The Otway Basin of southeastern Australia* (ed H Wopfner & J G Douglas), *Special Bulletin of the Geological Surveys of South Australia and Victoria, Adelaide*, 67-87.
- Harris W K 1985. Middle to Late Eocene depositional cycles and dinoflagellate zones in southern Australia. *Special Publications of the South Australian Department of Mines and Energy* 5:133-144.
- Haskell T R & Wilson G J 1975 Palynology of Sites 280-284, DSDP Leg 29, off southeastern Australia and western New Zealand. In: *Initial Reports of the Deep Sea Drilling Project* (ed J P Kennett, R E Houtz, *et al.*) 29, U S Government Printing Office, Washington, 723-741.
- Hocking R M 1990 Bremer Basin. In: *Geology and Mineral Resources of Western Australia*. Western Australia Geological Survey, *Memoir* 3:561-563.
- Hodgkin E P & Clark R 1989 Estuaries of the shire of Manjimup. *Estuarine Studies Series*, 6. Environmental Protection Authority, Perth.
- Hos D 1975 Preliminary investigation of the palynology of the Upper Eocene Werillup Formation, Western Australia. *Journal of the Royal Society of Western Australia* 58:1-14.
- Marshall N G & Partridge A D 1988 The Eocene acritarch *Tritonites* gen. nov. and the age of the Marlin Channel, Gippsland Basin, southeastern Australia. *Memoirs of the Association of Australasian Palaeontologists* 5: 239-257.
- McGowran B 1989 Silica burp in the Indian Ocean. *Geology* 17:887-860.
- Milne L. A 1988 Palynology of a late Eocene lignitic sequence from the western margin of the Eucla Basin, Western Australia. *Memoirs of the Association of Australasian Palaeontologists* 5:285-310.
- Partridge A D 1976 The geological expression of eustasy in the Early Tertiary of the Gippsland Basin. *APEA Journal* 16:73-79.
- Pearce R H & Barbeti M 1981 A 38000-year old archaeological site at Upper Swan, Western Australia. *Archaeology in Oceania* 16:173-178.
- Quilty P G 1978 The source of chert for Aboriginal artefacts in southwestern Australia. *Nature (London)* 275:539-541.
- Rock-Color Chart Committee 1963 *Rock-Color Chart*. Geological Society of America, New York.
- Stover L E 1975 Observations on some Australian Eocene dinoflagellates. *Geoscience and Man* 11:35-45.
- Stover L E & Partridge A D 1973 Tertiary and Late Cretaceous spores and pollen from the Gippsland Basin, southeastern Australia. *Proceedings of the Royal Society of Victoria* 85:237-286.
- Stover L E & Partridge A D 1982 Eocene spore-pollen from the Werillup Formation, Western Australia. *Palynology* 6:69-95.
- Williams G L & Bujak J P 1977 Cenozoic palynostratigraphy of offshore eastern Canada. *American Association of Stratigraphic Palynologists, Contribution Series* 5A:14-47.
- Wilson G J 1984 New Zealand Late Jurassic to Eocene dinoflagellate biostratigraphy - a summary. *Newsletters on Stratigraphy* 13:104-117.
- Wilson G L 1985 Dinoflagellate biostratigraphy of the Eocene Hampden Section, North Otago, New Zealand. *New Zealand Geological Survey Record* 8:93-101.

Water balance response in the terrestrial Western Australian frog, *Myobatrachus gouldii* (Anura: Myobatrachidae)

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Abstract

Dehydrated turtle frogs (*Myobatrachus gouldii*) slowly rehydrate in distilled water, reaching initial body mass after 160 min and 114% of initial mass after 450 min. The instantaneous rate of rehydration declined from the initial rate of $116 \text{ mg g}^{-1} \text{ h}^{-1}$ to $10 \text{ mg g}^{-1} \text{ h}^{-1}$ after 450 min. The turtle frog has the lowest rehydration rate measured from 16 Western Australian frogs, presumably reflecting the rarity of free water in its natural habitat and absence of a selective pressure for a marked water balance response. It has a large bladder volume, about 20% of body mass, and its urine is considerably more dilute than blood.

Introduction

The life history of most terrestrial amphibians is linked by their reproductive requirements to the presence of free-standing water. Almost invariably, eggs, tadpoles, or both stages require water for completion of development. Not surprisingly, iono- and osmoregulation by amphibians is controlled primarily by hydration across the skin from free-standing water, although many amphibians can absorb water from moist soil (Packer 1963, Bentley 1971, Bentley & Main 1972, McClanahan 1972, Shoemaker *et al.* 1992). The water balance response (WBR or Brunn effect) of amphibians is the restoration of body mass by the cutaneous reabsorption of water, primarily across the highly vascular pelvic skin under hormonal control by the posterior pituitary hormone, arginine vasotocin (AVT; Ewer 1952, Shoemaker & Waring 1968, Bentley 1971, Shoemaker *et al.* 1992). However, reproduction by some amphibians does not require free water; their eggs directly develop into froglets, without a free-swimming tadpole stage (Bogart 1981, Duellman & Trueb 1986). This reproductive strategy is used by two Australian frogs, the turtle frog *Myobatrachus gouldii* and *Arenophryne rotunda*, which deposit their eggs up to 1 to 2 metres underground (Roberts 1981, Roberts 1984).

Myobatrachus gouldii occurs in the south-western region of Western Australia, primarily in sandy soils of the Wandoo belt but not the forest regions (Tyler, Smith & Johnstone 1984). It is capable of surviving without free-standing water (How & Dell 1989). Individual turtle frogs might spend their entire life without ever encountering free-standing water, so

iono- and osmoregulation by these frogs must usually occur in the absence of free-standing water. Consequently, they might be expected to have a poor water balance response.

This study investigates the water balance response of turtle frogs, and determines whether it is lower than for other frogs and whether turtle frogs are able to maintain ionic and osmotic equilibrium in free-standing water.

Methods

Turtle frogs were collected from sandy sites east of Two Rocks, 55 km north of Perth, in November 1986 and returned to the laboratory in moist sand (approximately 1% water content) from the collection locality. All experiments were conducted as soon as possible after return to the laboratory.

Normally-hydrated individuals were washed free of sand, dried with paper towelling, and induced to urinate by inserting a polished glass cannula into the cloaca; the subsequent standard body mass was measured to $\pm 0.001 \text{ g}$ with a Sauter RL200 balance. The animals were then dehydrated overnight in dry containers by exposure to laboratory conditions. Body mass was reduced to approximately 80% of the standard mass. Individuals were then placed in a container with approximately 3 mm depth of distilled water, and reweighed at intervals, for up to 8 hours. The frogs were gently blotted dry with tissues and reweighed. Their bladders were not drained with each reweighing so that the water balance response could be suppressed naturally by the accumulation of bladder urine. The frogs usually did not urinate during the reweighing procedure if handled gently. If the weight of the frog decreased compared to a previous weighing indicating

that urine had been voided, then that weight was discarded from the analyses and further data were not collected. After the final reweighing, the bladder was drained and the frog reweighed to determine the volume (mass) of urine.

Blood and urine were collected from a sample of control, hydrated frogs (kept in moist sand) and the experimental frogs after dehydration/rehydration. The frogs were pithed, the ventricle exposed, incised with sharp scissors, and a blood sample collected directly into a heparinised capillary tube. The blood was centrifuged and the plasma separated and frozen for subsequent analysis. Urine samples were also frozen for subsequent analysis. Plasma and urine were analysed for Na^+ and K^+ using a Varian model 475 atomic absorption spectrophotometer. Cl^- was analysed using a Buchler-Cotlove amperometric titrator. NH_4^+ and urea concentrations were determined using a modified urease/alkaline hypochlorite/phenylnitroprusside spectrophotometric assay (Fawcett & Scott 1960). Osmotic concentration was determined using a Gonotek Osmomat freezing point osmometer.

Results

Initial body mass of the experimental turtle frogs was 7.46 ± 0.42 grams ($n = 7$), and dehydrated mass was 6.14 ± 0.37 grams (means values $\pm$ se); the dehydrated mass was $82.3 \pm 0.80\%$ of the initial mass. The turtle frogs slowly rehydrated when placed in distilled water, reaching initial body mass after about 160 minutes and about 114% of initial mass after 450 minutes (Fig 1).

The instantaneous rate of rehydration, calculated from the weight gain between consecutive weighings, declined from the initially highest rate of $116 \pm 14 \text{ mg g}^{-1} \text{ h}^{-1}$ to $19 \pm 2 \text{ mg g}^{-1} \text{ h}^{-1}$ after 450 minutes (Fig 2). The average rate of weight gain,

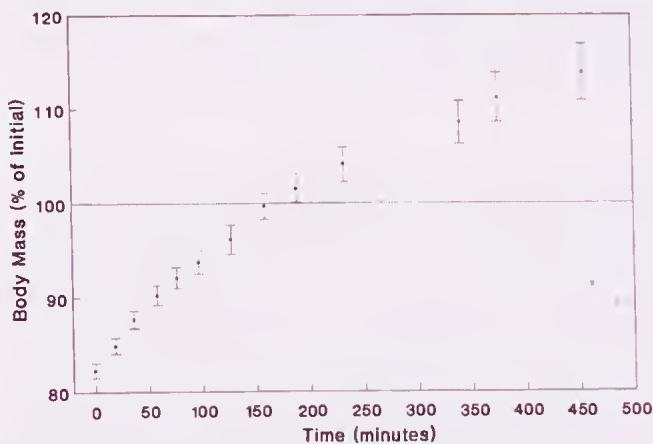


Figure 1 Increase in body mass of dehydrated turtle frogs *Myobatrachus gouldii*, after immersion in distilled water. Values are mean $\pm$ standard error, with the number of observations indicated.

calculated from the accumulated weight increase from the beginning of the experiment, also declined during rehydration from $116 \text{ mg g}^{-1} \text{ h}^{-1}$ for the first reweighing period, to $51 \text{ mg g}^{-1} \text{ h}^{-1}$ after 450 minutes.

The rate of rehydration would be expected to be proportional to the osmotic concentration difference between the body fluids and the ambient water (Shoemaker 1964). This

osmotic concentration difference should decline during rehydration as the body fluids are diluted by reabsorbed water, and so the instantaneous rehydration rate should

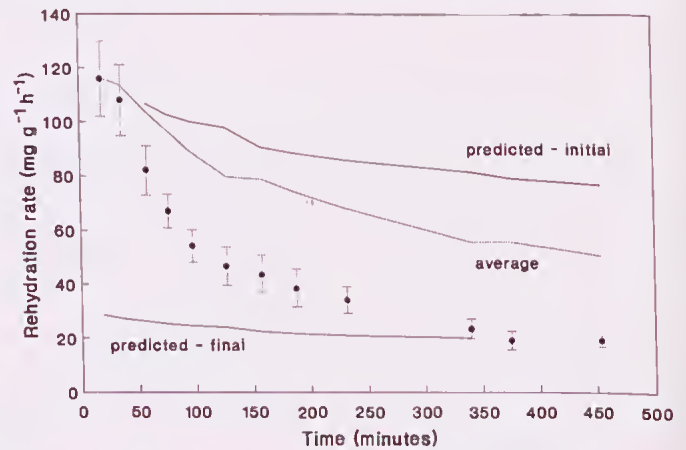


Figure 2. Instantaneous rehydration rate (solid circles; mean $\pm$ se, n) for dehydrated turtle frogs *Myobatrachus gouldii* immersed in distilled water. The average rehydration rate, calculated from the initial mass at time = 0, is also shown, along with the predicted rehydration rates (see text).

decline during rehydration. The effect of dehydration on body fluid osmotic concentration can be estimated from the weight loss. If we assume that the initial water content of the turtle frogs is 80% (see Main & Bentley 1964, Bentley *et al.* 1958 for body water content of other Australian frogs), then dehydration to 82.3% of initial weight would increase the body fluid osmotic concentration 1.28 times. Similarly, the body fluid osmotic concentration can be estimated from the body mass at any stage of rehydration. Figure 2 shows that the predicted decline in instantaneous rate of water uptake (calculated from the initial instantaneous rate of water uptake and the estimated osmotic gradient between body fluids and ambient distilled water during rehydration) does not decrease by as much as the actual rate of water uptake. Similarly, the predicted instantaneous rehydration rate calculated from the final observed rehydration rate (at 450 min) and the estimated osmotic concentration difference during rehydration does not decrease by as much as the actual rate of water uptake.

The average rehydration rate over the first 60 min is $31.1 \text{ mg cm}^{-2} \text{ h}^{-1}$ when expressed per calculated body surface area ($\text{cm}^2 = 6 \text{ grams}^{2/3}$; Bentley *et al.* 1958, Main & Bentley 1964). The ventral skin of *M. gouldii* is smooth, and so the calculated surface area was not corrected for granularity.

The urine volume of rehydrated turtle frogs ranged from 5.0 to 22.6% of body mass; the three highest values (15.7 , 20.1 and 22.6%) suggest a maximum bladder urine content of about 20% body mass.

The urine of hydrated, control frogs was significantly more dilute than plasma (Table 1). The Na^+ , K^+ and Cl^- concentrations were significantly lower for urine than plasma; there was no significant difference for NH_4^+ ; the urine concentration of urea was significantly greater than for plasma. There was no significant difference in osmotic or solute concentrations of plasma for dehydrated/rehydrated turtle frogs when compared to control frogs, except that plasma

Table 1

Osmotic and solute concentrations of plasma and urine for normally-hydrated turtle frogs *Myobatrachus gouldii* maintained in moist soil. Values are mean $\pm$ standard error with the number of observations in parentheses. The significance determined by t-test for the difference between plasma and urine values is indicated; ns = not significant, ** = $P < 0.001$.

	Plasma	Urine
Osmotic Concentration (mOsm kg ⁻¹)	225 $\pm$ 8 (10)	24.7 $\pm$ 2.1 (10)**
Na ⁺ Concentration (mM)	111 $\pm$ 3 (10)	4.2 $\pm$ 0.5 (6)**
K ⁺ Concentration (mM)	4.1 $\pm$ 0.6 (14)	1.7 $\pm$ 0.2 (10) ^{ns}
Cl ⁻ Concentration (mM)	84.1 $\pm$ 3.3 (9)	2.9 $\pm$ 0.6 (11)**
NH ₄ ⁺ Concentration (mM)	2.0 $\pm$ 0.2 (9)	1.5 $\pm$ 0.2 (9) ^{ns}
Urea Concentration (mM)	2.7 $\pm$ 0.4 (9)	12.7 $\pm$ 1.8 (9)**

urea concentration was higher (7.2 ± 0.7 mM, $n=7$, $P < 0.005$) for the dehydrated/rehydrated frogs. The urine of dehydrated/rehydrated turtle frogs had a significantly higher osmotic concentration (47.2 ± 5.6 mOsm, $n=6$, $P < 0.005$), Na⁺ concentration (10.7 ± 3.0 mM, $n=6$, $P < 0.05$), K⁺ concentration (3.2 ± 0.8 mM, $n=7$, $P < 0.05$) and urea concentration (26.1 ± 4.2 mM, $n=6$, $P < 0.01$) than for normal frogs.

Discussion

Amphibians absorb water across their skin when placed in fresh water, but the rate of cutaneous water influx varies with temperature, body size and species (Shoemaker & Nagy 1977, Shoemaker *et al.* 1992). Terrestrial amphibians tend to have high water influx rates to maximize the rate of rehydration when water is available, whereas aquatic species tend to have low water influx rates to minimise osmotic disturbance to the body fluid composition (Ewer 1952, Schmidt 1965, Bentley 1971, Shoemaker *et al.* 1992, Boutilier *et al.* 1992).

Turtle frogs, dehydrated to 82% of initial mass, rehydrated to initial body mass after about 160 min, and by 450 min had reached 114% of initial body mass (Fig 1). The overshoot in body mass might indicate an inability of turtle frogs to maintain osmotic homeostasis in the unnatural situation of immersion in distilled water. However, rehydration after 450 min had not yet restored the normal plasma urea concentration, and the urine of dehydrated/rehydrated frogs still had higher osmotic, Na⁺, K⁺ and urea concentrations than urine of normal frogs.

The instantaneous rate of rehydration declined markedly from the initial high value of $116 \text{ mg g}^{-1} \text{ h}^{-1}$, to $25 \text{ mg g}^{-1} \text{ h}^{-1}$

after 450 min (Fig 2). The instantaneous rate of rehydration did not decline with the predicted osmotic gradient for either the initial or final rehydration rate. This indicates that another non-osmotic control factor rapidly reduces the rehydration rate from the initial high value. The neurohypophyseal hormone AVT is one such potent regulator of cutaneous osmotic permeability and rehydration rate (Ewer 1952, Bentley 1971, Shoemaker *et al.* 1992).

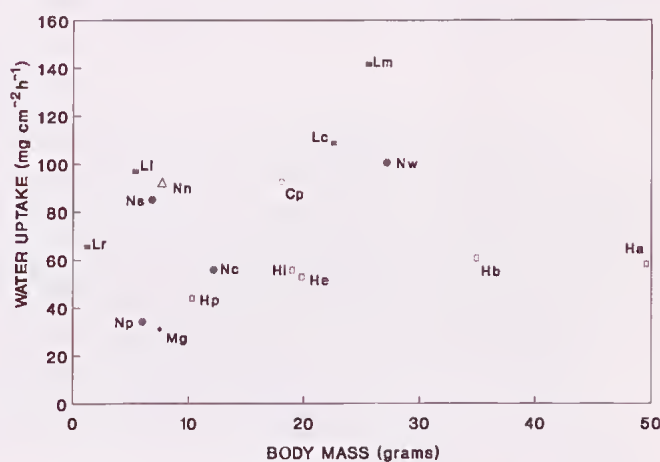


Figure 3. Comparison of rehydration rate (initial 60 min) for a variety of Western Australian amphibians, *Myobatrachus gouldii* (Mg, present study), *Neobatrachus pelobatoideus* (Np), *N. centralis* (Nc), *N. wilsmorei* (Nw), *N. sutor* (Ns), *Heleioporus psammophilus* (Hp), *H. inornatus* (Hi), *H. eyrei* (He), *H. barycragus* (Hb), *H. albopunctatus* (Ha), *Notaden nichollsi* (Nn), *Cyclorana platycephala* (Cp), *Litoria rubella* (Lr), *L. latopalmata* (LI), *L. caerulea* (Lc) and *L. moorei* (Lm); values from Bentley *et al.* (1958) and Main & Bentley (1964).

The average rehydration rate measured for *Myobatrachus gouldii* of $31.1 \text{ mg cm}^{-2} \text{ h}^{-1}$ (over the first 60 min of rehydration from 20% mass loss) is the lowest determined under comparable conditions for 15 species of Western Australian frogs from 4 genera (Bentley *et al.* 1958, Main & Bentley 1964; Fig 3). There is no obvious relationship between area-specific water uptake rate and body mass for these various Western Australian species. Bentley *et al.* (1958) reported a significant relationship between rehydration rate and environmental aridity for species of *Neobatrachus* (which dig shallow burrows in clay soil), but not for *Heleioporus* species (which dig deep burrows in sandy soil). Main & Bentley (1964) reported high rates of rehydration for some treefrogs (*Litoria moorei*, *L. caerulea* and *L. latopalmata*) and a desert burrowing frog, *Cyclorana platycephala*, which is closely related to tree frogs like *L. moorei* (Maxson *et al.* 1982, 1985). The lowest rehydration rates are for species which deeply burrow in sandy soils (*Heleioporus* spp, *Notaden nichollsi* and *Myobatrachus gouldii*); of these, only *Notaden* voluntarily enters water after metamorphosis to breed (Main 1968). The low rehydration rate of *Myobatrachus gouldii* presumably reflects the absence or rarity of free water in its natural habitat and lack of selective pressure for a marked water balance response.

The urinary bladder capacity of *M. gouldii* is about 20% body mass. This is greater than the bladder volume of aquatic frogs (about 1-5%) but is less than the extreme values of about 30-50% for some terrestrial, arid-adapted frogs (see

Shoemaker *et al.* 1992). The urine of *M. gouldii* is relatively dilute compared to plasma for both normally-hydrated frogs (Table 1) and dehydrated/rehydrated frogs. Consequently, bladder urine would be an important water store for *M. gouldii* during dry periods.

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References

- Bentley PJ 1971 Endocrines and Osmoregulation. A Comparative Account of the Regulation of Salt and Water in Vertebrates. Springer Verlag, New York.
- Bentley PJ, Lee AK & Main AR 1958 Comparison of dehydration and hydration of two genera of frogs (*Heleioporus* and *Neobatrachus*) that live in areas of varying aridity. *Journal of experimental Biology* 35:677-684.
- Bentley PJ & Main AR 1972 Effect of vasotocin on cutaneous water uptake by an Australian frog, *Crinia georgiana*. *Copeia* 1972:885-886.
- Bogart JP 1981 How many times has terrestrial breeding evolved in anuran amphibians? *Monitore Zoologico Italiano Supplemento* 15:29-40.
- Boutilier RC, Stiffler DF & Toews DP 1992 Exchange of respiratory gases, ions, and water in amphibious and aquatic amphibians. In: *Environmental Physiology of the Amphibia* (ed M E Feder & W W Burggren) University of Chicago Press, Chicago, 81-124.
- Duellman WE & Trueb L 1986 *Biology of Amphibians*. McGraw-Hill, New York.
- Ewer RF 1952 The effect of pituitrin on fluid distribution in *Bufo regularis* (Reuss). *Journal of experimental Biology* 29:173-177.
- Fawcett JK & Scott JE 1960 A rapid and precise method for the determination of urea. *Journal of Clinical Pathology* 13:156-159.
- How RA & Dell J 1989 Vertebrate fauna of *Banksia* woodlands. *Journal of the Royal Society of Western Australia* 71:97-98.
- Main AR 1968 Ecology, systematics and evolution of Australian frogs. *Advances in Ecological Research* 5:37-86.
- Main AR & Bentley PJ 1964 Water relations of Australian burrowing frogs and tree frogs. *Ecology* 45:379-382.
- Maxson LR, Ondrula DP & Tyler MJ 1985 An immunological perspective on evolutionary relationships in Australian frogs of the hylid genus *Cyclorana*. *Australian Journal of Zoology* 33:17-22.
- Maxson LR, Tyler MJ & Maxson RD 1982 Phylogenetic relationships of *Cyclorana* and the *Litoria aurea* species-group (Anura: Hylidae): a molecular perspective. *Australian Journal of Zoology* 30:643-651.
- McClanahan LL 1972 Changes in body fluids of burrowed spadefoot toads as a function of soil water potential. *Copeia* 1972:209-216.
- Packer WC 1963 Dehydration, hydration, and burrowing behavior in *Heleioporus cyrei* (Gray) (Leptodactylidae). *Ecology* 44:643-651.
- Passmore NI & Carruthers VC 1979 *South African frogs*. Witwatersrand University Press, Johannesburg.
- Roberts JD 1981 Terrestrial breeding in the Australian leptodactylid frog *Myobatrachus gouldii* (Gray). *Australian Wildlife Research* 8:451-462.
- Roberts JD 1984 Terrestrial egg deposition and direct development in *Arenophryne rotunda* Tyler: a myobatrachine frog from coastal sand dunes at Shark Bay, Western Australia. *Australian Wildlife Research* 11:451-462.
- Schmidt WD 1965 Some aspects of the water economies of nine species of amphibians. *Ecology* 46:261-269.
- Shoemaker VH 1964 The effects of dehydration on electrolyte concentrations in a toad, *Bufo marinus*. *Comparative Biochemistry & Physiology* 13:261-267.
- Shoemaker VH & Waring H 1968 Effect of hypothalamic lesions on the water-balance response of a toad (*Bufo marinus*). *Comparative Biochemistry and Physiology* 24:47-54.
- Shoemaker VH, Hillman SS, Hillyard SD, Jackson DC, McClanahan LL, Withers, PC & Wygoda ML 1992 Exchange of water, ions, and respiratory gases in terrestrial amphibians. In: *Environmental Physiology of the Amphibia* (ed M E Feder & W W Burggren) University of Chicago Press, Chicago, 125-150.
- Shoemaker VH & Nagy KA 1977 Osmoregulation in amphibians and reptiles. *Annual Reviews of Physiology* 39:449-471.
- Tyler MJ, Smith LA & Johnston R 1984 *Frogs of Western Australia*. Western Australian Museum, Perth.

Holocene vegetation and climate record from Barker Swamp, Rottnest Island, Western Australia

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Abstract

Palynological and lithological study of a core taken from Barker Swamp, Rottnest Island shows that between 7500 and 6600 years B.P. peat was deposited in an open freshwater lake surrounded by sedges and *Callitris* low forest, with a restricted jarrah/tuart woodland present nearby. Above the peat banded calcilutite sediments contain a succession of charcoal-rich horizons. These are the result of fires that largely destroyed the *Callitris* low forest and caused other elements of the vegetation to decline. The subsequent period of cream-coloured calcilutite deposition started approximately 5300 years B.P. and contains evidence for increased aridity and sparser vegetation. At this level, *Pimelea* and *Asteraceae* are dominant in the pollen profile and eucalypts decline to abundances consistent with pollen blown from the mainland. *Casuarina* persists as a significant minor element in the pollen profile to the top of the calcilutite interval. A large increase in charcoal and organic material marks the start of European settlement. Later stages of settlement are indicated by increased pollen from eucalypt, *Callitris* and *Melaleuca lanceolata*, a consequence of reforestation on Rottnest Island after 1932.

Introduction

Rottnest Island lies 18 km west of the mainland of Western Australia, offshore from the Perth metropolitan area. It is a hilly, scrub-covered island of approximately 1900 ha, with a series of salt lakes occupying a large portion of the central-eastern part.

The island lies at the northern end of a chain of reefs and islands, formed by Pleistocene Tamala Limestone, that runs south to the mainland through Garden Island. The island chain originally formed a land connection to the mainland; a connection severed about 6500 years ago during the Flandrian transgression (Playford 1988). Recent accounts of the geology of Rottnest Island are provided by Playford & Leech (1977) and Playford (1988).

Eight freshwater, or previously freshwater, swamps exist on the island at the present day (Fig 1): five of these, Barker, Salmon, Lighthouse, Bulldozer, and Parakeet Swamps, are interdunal and two, Bickley and Rifle Range Swamps, both at the eastern end of the island, have been described as shell-flat swamps (Hassell & Kneebone 1960). Most of the swamps were mined for road-building material during the early 1970s and are now hypersaline lakes, but Barker and Rifle Range Swamps were not, probably because of their distance from existing sealed roads. Another unnamed swamp lies to the west of Bickley Swamp (Fig 1). This swamp is thought to be undisturbed and is probably a shell-flat swamp.

The objective of the present study was to examine the pollen record from Barker Swamp for comparison with an earlier pollen study of Lighthouse Swamp reported by Hassell & Kneebone (1960) and Churchill (1960). The study was also intended to demonstrate the potential of Quaternary pollen as a record of recent climatic changes in the Perth region.

Barker Swamp (lat 32° 0' 8"S, long 115° 30' 11"E) occupies approximately one hectare and lies in a hollow near the centre of Rottnest Island, at an elevation of less than 1 m above sea-level. The swamp is bounded immediately to the north by a 25 m high ridge of Pleistocene Tamala Limestone, and to the east, south and west by lower undulating areas of sand covered limestone. It contains the largest undisturbed area of swampland and the greatest known thickness of Holocene sediments of any swamp on the island.



Figure 1. Location of swamps on Rottnest Island.

Vegetation history since European observation

Early observations on the vegetation of Rottnest are summarized by Pen and Green (1983). Reports by Volkersen in 1658, Freycinet in 1801 and Cunningham in 1822 indicate a dense cover of woods and thickets, and in particular the presence of large stands of *Callitris preissii* (Rottnest Island pine). Pen and Green (1983) conclude from these reports that *Callitris* was abundant in the eastern part of the island, but the western part may have consisted of sparsely vegetated sand dunes (Wilson 1829, quoted in Marchant & Abbott 1981).

Forest clearing followed European settlement of the island in 1831. *Callitris* was felled for timber and frequent fires extensively modified the vegetation. *Callitris preissii* and *Melaleuca lanceolata* are not fire tolerant and were extensively reduced. *Acacia rostellifera*, which regenerates after fire by producing suckers, replaced *Callitris* and *Melaleuca* to form dense thickets (Pen & Green 1983). Storr (1963) attributed the decline of *Acacia* scrub since 1930 to a combination of repeated fires and increased grazing by quokkas (*Setonix brachyurus*) since their protection from hunting in the late 1920s. A large fire in 1955 affected the central western part of the island, presumably including the Barker Swamp area. This hastened the spread of *Acanthocarpus-Stipa*, low, dense heath which now covers the hills to the north, west, and east of Barker Swamp. Since 1932 eucalypts, *Melaleuca* and *Callitris* have been established in a number of plantations, and exotic species, including Norfolk Island pines, have been planted sporadically in the Thompson Bay area and elsewhere. A plantation of *Acacia rostellifera* and *Melaleuca lanceolata* occupies low ground within 50 m of the southern margin of Barker Swamp.

Previous studies

Studies of Quaternary pollen on Rottnest Island form part of an unpublished thesis by Hassell & Kneebone (1960) and a brief paper by Churchill (1960).

Hassell put down auger holes in two shell-flat swamps (Bickley and Rifle Range) and four interdunal swamps (Barker, Lighthouse, Salmon and Parakeet) (Fig 1). He considered that the stratigraphy in all the interdunal swamps was essentially similar, despite the differences in thicknesses of individual lithologic units between swamps. Hassell's stratigraphy for the interdunal swamps can be summarized as follows:

1. Upper Peat - approximately 10 cm.
2. Buff Calcilutite.
3. White Calcilutite.
4. Algal Banded Calcilutite - essentially mottled grey and pink calcilutite.
5. Lower Peat.

In Lighthouse Swamp he demonstrated that all lithologic units extend across the swamp and thin significantly towards the margins. Hassell & Kneebone (1960) presented a table showing fossil pollen as a percentage of total pollen for five samples, one sample from each of the stratigraphic units listed above, from an auger hole in Lighthouse Swamp. The Lower Peat, Algal Banded Calcilutite and White Calcilutite pollen spectra are dominated by Chenopodiaceae and Cyperaceae. The Buff Calcilutite contains common Chenopodiaceae, Poaceae, Cyperaceae and Euphorbiaceae, and the Upper Peat contains 98% Chenopodiaceae. Eucalypt pollen is present at all levels, but is most abundant in the Lower Peat (5%) and the Buff and White Calcilutite (4% and 6% respectively). Only 100 pollen in total were counted for each sample, and therefore the eucalypt pollen count is too small to be statistically significant.

Churchill (1960) presented fossil pollen data, evidently based largely on the work of Hassell. Churchill also compared the fossil pollen record from Lighthouse Swamp and

Serpentine Lake with the modern (c.1960) atmospheric pollen count at the Rottnest Island Biological Research Station, and at an unspecified location on the adjacent mainland. Among other conclusions, he suggested that eucalypt pollen gradually decrease through the sedimentary record, and the number of eucalypts present on the island during the early period of peat deposition was similar to the number on Rottnest in about 1960. He also observed that *Callitris* pollen is abundant in the fossil record, although it was not recorded by Hassell.

Churchill (1960) reported a date on a fossil blackboy (*Xanthorrhoea*) stump from a depth of 19ft (5.75m) at an unknown locality on the island. It was dated at 7090 ± 115 yr B.P. He also recorded the find of a piece of *Callitris* wood in the "Rottnest Shell Beds", now called the Herschell Limestone.

The statement by Storr *et al.* (1959) that "a tuart woodland similar to that of the present mainland once existed" on Rottnest is presumably based on the evidence subsequently presented by Hassell & Kneebone, (1960) and Churchill (1960) and discussed above. This conclusion has been restated several times, most recently by Pen and Green (1983) and Playford (1988). It relies on the undoubted former presence of *Xanthorrhoea* and the perceived greater abundance in the fossil record of species typical of tuart woodland, including several species of *Eucalyptus*.

Methods

Samples were collected for the present study using a post-hole digger with a 13 cm cut, a hand auger and a hand operated, D-section corer.

Two test holes were used at Barker Swamp to ascertain the sedimentary thickness and the best methods of sample collection in the different lithologies. In the third hole, Barker Swamp 3, cores were cut down to the top of the Lower Peat and the hole continued by auger through the peat to the underlying sand.

The upper layers of calcilutite were too stiff to allow full 50 cm cores to be cut using the D-section corer. In this lithology the hole was widened with the post-hole digger after each short run (usually less than 30 cm) for easier access. Cores were taken alternately from opposite sides at the bottom of the widened hole. In the Banded Calcilutite and upper part of the Lower Peat the sediments were soft enough to permit full 50 cm cores to be taken on each run and hole widening was unnecessary. The depth of each core-run was carefully measured from the swamp surface and each core overlaps the previous core by at least 12 cm. Fourteen cores were cut in Barker Swamp 3 between 16 and 329 cm, and the surface material to a depth of about 20 cm was sampled with a spade. The corer had only sufficient extension rods to reach 329 cm. Below this depth samples were collected with the hand auger to a depth of 401 cm. A set of near surface samples were collected from a small trench.

Some core samples were obtained for comparative purposes from Salmon Swamp. In this swamp, banded calcilutite and sandy peat extend for 158 cm below the excavated surface before grey sand is reached.

Samples were prepared using standard acetolysis methods as outlined by Faegri & Iversen (1975) and Moore & Webb (1978), with brief oxidation used on some samples. Initially

glycerine jelly was used as a mounting medium, but later preparations were mounted in silicone oil. *Lycopodium* tablets, either whole or in solution, were added to allow estimation of the pollen concentration.

In the peat sections, 1 cm³ of sample was sufficient to produce enough organic material for analysis. In the Banded Calcilutite 2 or 3 cm³ of sample was used, and in the calcilutite 4 cm³ of sample was required.

Dinoflagellate cysts are abundant in many samples in the Banded Calcilutite and Calcilutite. They were counted up to the first 25 or 50 *Lycopodium* spores. Pollen groups were usually counted up to 100 *Lycopodium* spores. In most samples a minimum of 200 pollen grains were counted, in a few sparse samples counts were between 100 and 200, and in two samples (16.5 and 18.5 cm) because of the infrequency of pollen fewer than 100 were counted.

Many of the rarer taxa could not be identified unequivocally to family level. Fortunately, the most common pollen taxa are well known at family or generic level because of their frequency in Quaternary deposits.

Radiocarbon dates from Barker Swamp

A pooled group of auger samples from slightly above the base of the peat in Barker Swamp 3 gave a conventional radiocarbon date of 7220 ± 210 yrs B.P., and a sample from core 13 (302-309 cm), near the top of the peat, gave a date of 6850 ± 360 yrs B.P. Accelerator mass spectrometry dating of a small sample from the 197 cm charcoal band gave a date of 5645 ± 72 yrs B.P. (NZA 2774) (Fig 4).

Stratigraphy of Barker Swamp

The Barker Swamp sequence is divided here into four broad lithologic units. In descending order these are:

Surface Peat	0 - 13 cm
Calcilutite	13 - 169 cm
Banded Calcilutite	169 - 296 cm
Lower Peat	296 - 394 cm

Significant variation occurs within each unit (Fig 2). The Lower Peat is underlain below 394 cm by medium grained, grey, quartzose sand, which probably overlies Tamala Limestone at depth.

The Lower Peat, from 296 to 394 cm, consists predominantly of black to dark brown peat with clearly distinguishable fragments of leaves that appear to be mainly Cyperaceae. Abundant molluscs, ostracods, and fine shell material impart a silty appearance to the lower part. Ostracods and fine shell material are less frequent in the upper part where dense black peat predominates. The fine organic maceral content of the Lower Peat includes occasional charcoal, frequent algal filaments and fungal spores, and abundant fibrous leaf and stem remains. *Botryococcus* and *Pediastrum* are present at some levels.

The Banded Calcilutite interval extends between 169 and 296 cm. It consists of a series of thin, dark-grey, charcoal-rich bands, usually overlain by chocolate-brown, fine-grained calcilutite (essentially a lime mud with varying minor amounts of organic material), interbedded with thicker

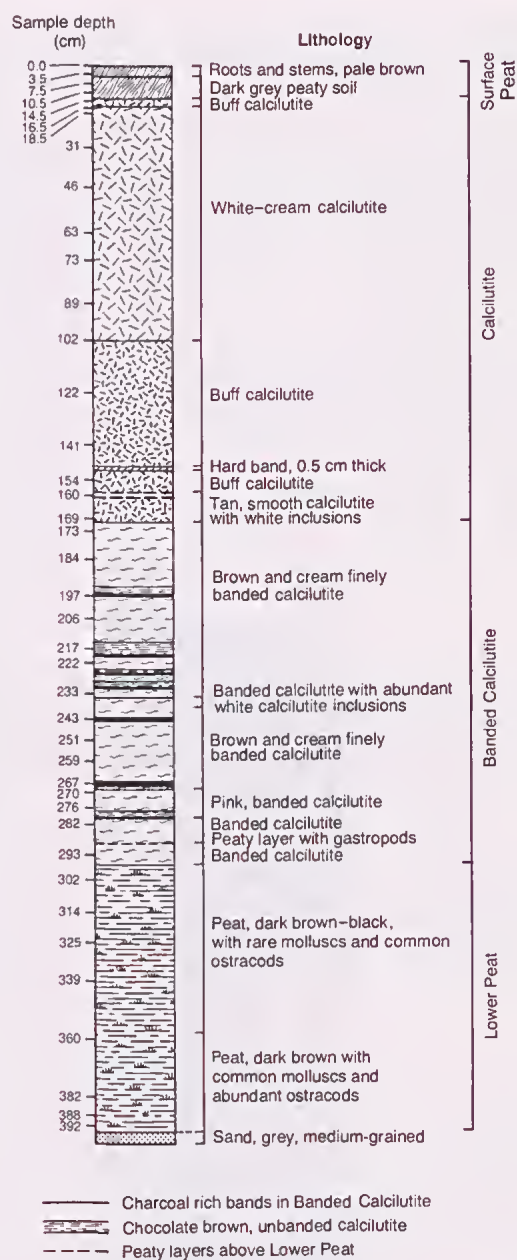


Figure 2. Lithologic column for Barker Swamp 3.

intervals of finely banded sediments. A thin layer of peaty material with abundant shells of the snail *Physastra* occurs at 289 cm, a short distance above the Lower Peat. The base of each major charcoal band is sharply delineated and the upper boundary is diffuse, with charcoal fragments reducing gradually up section. Major charcoal rich bands occur at 279, 267, 243, and 197 cm. Less prominent charcoal bands are clustered between 215 and 235 cm (Fig 2). In some intervals of the Banded Calcilutite, where the banding is well defined, individual fine bands can be distinguished and counted. Each band is 0.75-1.5 mm thick and consists of cream-coloured calcilutite overlain by a brown, organic-rich layer. The interval between 269 and 277 cm is a distinctive pink colour, in contrast to the brown colour of the Banded Calcilutite in other intervals.

Charcoal is more common at all levels in the Banded Calcilutite than in the Lower Peat. In the charcoal-rich bands it is often the dominant maceral. In banded intervals, *Botryococcus*, amorphous algal material, and small,

subspherical algal cysts comprise the bulk of the organic material. Dinoflagellate cysts are abundant in several samples in the upper part above 259 cm.

The sequence of light and dark layers, produced by variation in charcoal content, in the lowest part of the Banded Calcilutite in Barker Swamp is replicated in the corresponding interval in Salmon Swamp. Figure 3 shows the lower Banded Calcilutite interval in Barker Swamp between 248 and 296 cm, with the top of the Lower Peat, and the 279 and 267 cm charcoal bands indicated. The equivalent interval in Salmon Swamp is shown alongside. The major fires that affected Barker Swamp also appear in the sedimentary record of Salmon Swamp, 1 km to the south, evidence that these were substantial fires. The similarity in the banding pattern between the two cores suggests that it may be possible to finely correlate the entire Banded Calcilutite interval between these two sites.

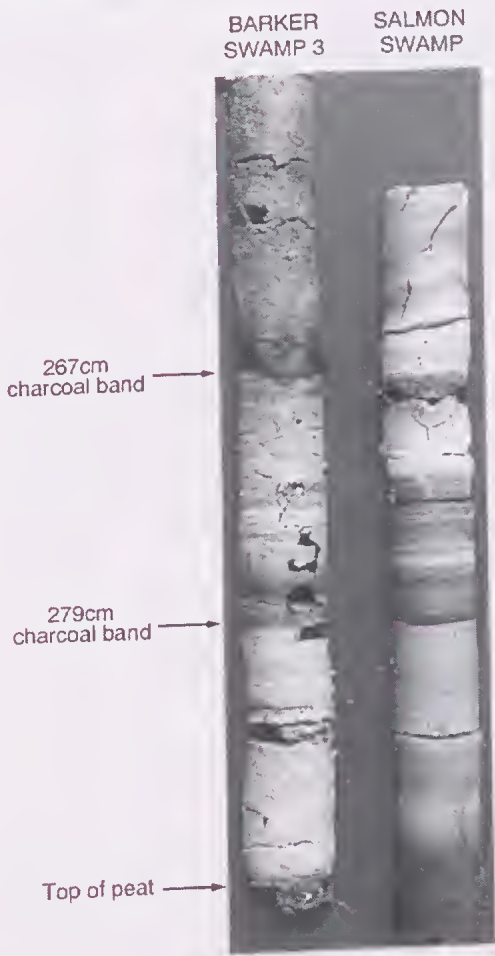


Figure 3. Comparison of the lowest Banded Calcilutite intervals in cores from Barker Swamp and Salmon Swamp.

The boundary between the Banded Calcilutite and the overlying Calcilutite is transitional. Visible organic fragments decrease gradually as banded calcilutite gives way to pale, chocolate-coloured calcilutite. The interval included in the Calcilutite is from 13 to 169 cm. Buff-coloured calcilutite occurs predominantly in the lower part, in contrast to the swamp stratigraphy outlined by Hassell & Kneebone (1960). Lithologically the Calcilutite consists of white to cream, or buff-coloured, chemically precipitated, lime mud, with abundant ostracod carapaces. At the top, a narrow band of

buff-coloured calcilutite immediately underlies the dark Surface Peat. Cream-coloured calcilutite extends down to 102 cm, and below 102 cm the calcilutite becomes buff-coloured and then chocolate brown. Two thin, slightly peaty, horizons occur at a depth of about 160 cm.

A hard band of semi-cemented calcilutite, 0.5 cm thick, occurs at 143 cm, and less cemented hard bands occur just above this level. A better developed hard band is present in Salmon Swamp at a depth of 78 to 79 cm below the excavated surface, in a similar stratigraphic position to the hard band in Barker Swamp. These hard bands are assumed to indicate a period of desiccation that affected both swamps.

Charcoal is infrequent in the Calcilutite. In the lower part dinoflagellate cysts and amorphous algal material are still common and in the highest part, between 16.5 and 63 cm, small subspherical algal cysts dominate the assemblages. This changes abruptly in the 14.5 cm sample, in buff calcilutite, where amorphous algal material, leaf remains, and charcoal are more frequent.

The carbonaceous interval between the surface and 13 cm is referred to as the Surface Peat, although it is not a true peat. It can be subdivided into a lower layer of charcoal rich, dark grey, sandy, calcareous sediment between 5 and 13 cm and an upper, pale brown, spongy layer, with less frequent charcoal and composed largely of *Sarcocornia* roots and stems.

Microfauna

Ostracods and molluscs were examined from 8 samples in Barker Swamp 3. Species presence at different sample depths is shown in Table 1.

De Deckker (pers comm. 1991) considers that *Mytilocypris tasmanica chapmanii*, *M. ambigua*, *Diacypsis spinosa*, and *Cyprideis* aff. *australiensis* tolerate slightly saline water. These species are present in the Banded Calcilutite and Calcilutite, but only *C. aff. australiensis* is also present in the Lower Peat. The other species recovered from the Lower Peat favour fresh-water conditions; *C. tenuis* can tolerate swampy conditions and *K. cristata* is often associated with oligotrophic conditions. From the abundance of the latter species in the Lower Peat it is concluded this unit was deposited in a small, open, freshwater lake.

	Surface	92-98 cm	123-131 cm	165 cm	230-262 cm	314-317 cm	358-363 cm	386-394 cm
Ostracoda								
<i>Alboa worooa</i>	A							
<i>Mytilocypris tasmanica chapmanii</i>	C	C	C		R			
<i>M. ambigua</i>								
<i>Diacypsis spinosa</i>		R		R	R			
<i>Cyprideis</i> aff. <i>australiensis</i>		R		R	A	R	R	R
<i>Kennethia cristata</i>						A	C	C
<i>Candonopsis tenuis</i>						R		R
Mollusca								
<i>Coxiella striatula</i>	A							
<i>Physastra</i> sp.						C	C	R
<i>Ferrissia</i> sp.						C	C	R
cf. <i>Paraloma</i> sp.								R
<i>Austrosuccinea</i> sp.								R
Gastropod sp. A (<i>Canthiacea</i>)								R

Table 1.

Stratigraphic distribution of ostracods and molluscs in Barker Swamp 3; A, abundant; C, common; R, rare.

Edward (1983) related several of the above ostracods to water salinity in a study of fauna from inland waters on Rottnest. *K. cristata*, *A. worooa* and *M. ambiguosa* are present in the salinity range 1 - 14.8 ppm, and *D. spinosa* has a salinity range of 2.4 - 44.0 ppm.

Of the molluscan fauna, *Physastra* is a pond snail known from fresh and brackish waters, and *Ferrissia* is a freshwater limpet. *Austrosuccinea* and cf. *Paraloma* sp. are terrestrial snails washed into the lake. *Coxiella striatula* is common in saline and brackish inland waters.

Pollen diagram

The pollen diagram for Barker Swamp (Fig 4) indicates significant changes in the vegetation at this locality over the past 7500 years. The greatest changes approximate the major lithologic boundaries outlined above. Pollen taxa are shown as a percentage of the total pollen spectra. A few pollen types that are extremely rare and unidentified taxa, which comprise less than 2% of total pollen in most samples, are not shown.

In this study, *Eucalyptus* type A includes pollen that is probably *E. gomphocephala* (tuart), *E. marginata* (jarrah) and *E. tottiana*, taxa whose pollen seems to be rather similar in appearance. All other eucalypt pollen is categorized together. Because of special interest in the previous presence of eucalypts on the island, the *Eucalyptus* pollen concentration is also given as this better illustrates the actual abundance of this pollen type in the sediments.

The pollen characteristics of the four lithologic units are summarized below:

Lower Peat: Pollen concentration low at the base, increasing to the top; *Callitris* and Cyperaceae high to moderate; Asteraceae, *Casuarina*, Poaceae, Restionaceae, Rutaceae and *Eucalyptus* low. *Pimelea* absent. *Xanthorrhoea* present at 392 cm and a single *Banksia* at 339 cm

Banded Calcilutite: Pollen concentration initially high, decreasing to the top; *Callitris* high to low; Asteraceae, Chenopodiaceae, *Eucalyptus* and *Pimelea* (in upper part) moderate to low; Cyperaceae, *Casuarina*, Poaceae, Restionaceae, Rutaceae, Portulacaceae and *Melaleuca* low.

Calcilutite: Pollen concentration extremely low; *Pimelea* and Asteraceae relatively high; *Casuarina*, *Eucalyptus*, Restionaceae and Chenopodiaceae low to moderate; Cyperaceae, Rutaceae and *Melaleuca* low; *Callitris* absent.

Surface Peat: Pollen concentration high; Chenopodiaceae extremely high; *Eucalyptus* and *Melaleuca lanceolata* low; Cyperaceae, Asteraceae, *Casuarina*, Poaceae, Restionaceae and Rutaceae present, but very rare; *Pimelea* absent. *Acacia* present in surface sample.

History of Barker Swamp

Sedimentation at the Barker Swamp site commenced with the establishment of a fresh, open water lake approximately 7500 yrs B.P., near the end of the sea-level rise that followed the last glaciation and which eventually separated Rottnest Island from the mainland (Playford 1988). The lake contained a diverse freshwater fauna and occasional dinoflagellates. It was surrounded by sedges (Cyperaceae), probably *Galnina*

trifida and *Isolepis nodosa* the most common species extant on Rottnest. *Callitris preissii* dominated the vegetation beyond the fringes of the lake, and probably formed a low forest similar to the *C. preissii* low forest still present on Garden Island. *Casuarina* and *Eucalyptus* were less common or more distant elements of the vegetation. *Xanthorrhoea* was present in the vicinity of the swamp for at least the first two or three hundred years, while melaleucas, including *M. lanceolata*, were rare elements of the flora.

Limited evidence from the lower peaty layer in Salmon Swamp, where Chenopodiaceae pollen is abundant, indicates that this swamp was more saline than Barker Swamp during the Lower Peat period. This accords with the pollen record from the Lower Peat in Lighthouse Swamp (Hassell & Kneebone 1960)

On the assumption that peat accumulation in Barker Swamp ended approximately 6600 yrs B.P., the rate of accumulation of the Lower Peat is estimated at about 10 cm per 100 yr.

Open freshwater swamp conditions gave way to rather more brackish conditions and deposition of calcilutite with thin organic-rich bands. A peaty layer with freshwater gastropods at 287 cm represents a brief return to the conditions that prevailed during deposition of the peat. The change in sedimentary regime is coeval with the disappearance of freshwater molluscs, and the ostracod fauna shifted towards species more tolerant of brackish water. At the swamp margin, sedges declined and salt-tolerant chenopods increased. *Callitris* still dominated the surrounding area, and *Eucalyptus*, *Casuarina*, *Melaleuca*, Poaceae, Restionaceae and Rutaceae (particularly *Diplolaena*) gradually became more common.

A fire, represented by the charcoal band at 279 cm, appears to have had little effect on the overall abundance of *Callitris*, but a subsequent and probably larger fire, represented by the 267 cm charcoal band, dramatically reduced the number of *Callitris*. A further major fire, indicated by the 243 cm charcoal band, and a series of smaller fires, represented by a series of thinner charcoal bands up to 185 cm, eliminated most of the *Callitris* in the Barker Swamp area. However, a few *Callitris* regenerated and survived, as evidenced by the presence of *Callitris* pollen near the top of the Banded Calcilutite interval at 173 cm.

The concentration of eucalypt pollen decreases significantly above the charcoal bands at 279 and 267 cm, from which it is concluded that the eucalypts, as well as *Callitris preissi*, were seriously affected by these fires.

The charcoal band at 267 cm is followed by an increase in the percentage of Chenopodiaceae and Asteraceae pollen, but it is not certain that this represents an actual increase in frequency of these taxa because the pollen concentration falls sharply at this level. *Pimelea* pollen appear in the record for the first time between the 267 and 279 cm fires, and increase in relative abundance to become the dominant taxon in the pollen record by the top of the Banded Calcilutite. By this time vegetation in the area of Barker Swamp was predominantly low scrub with occasional *Callitris*, *Eucalyptus* and possibly *Casuarina*. The land connection with the mainland was probably severed during the Banded Calcilutite period. The subsequent removal of population controls on

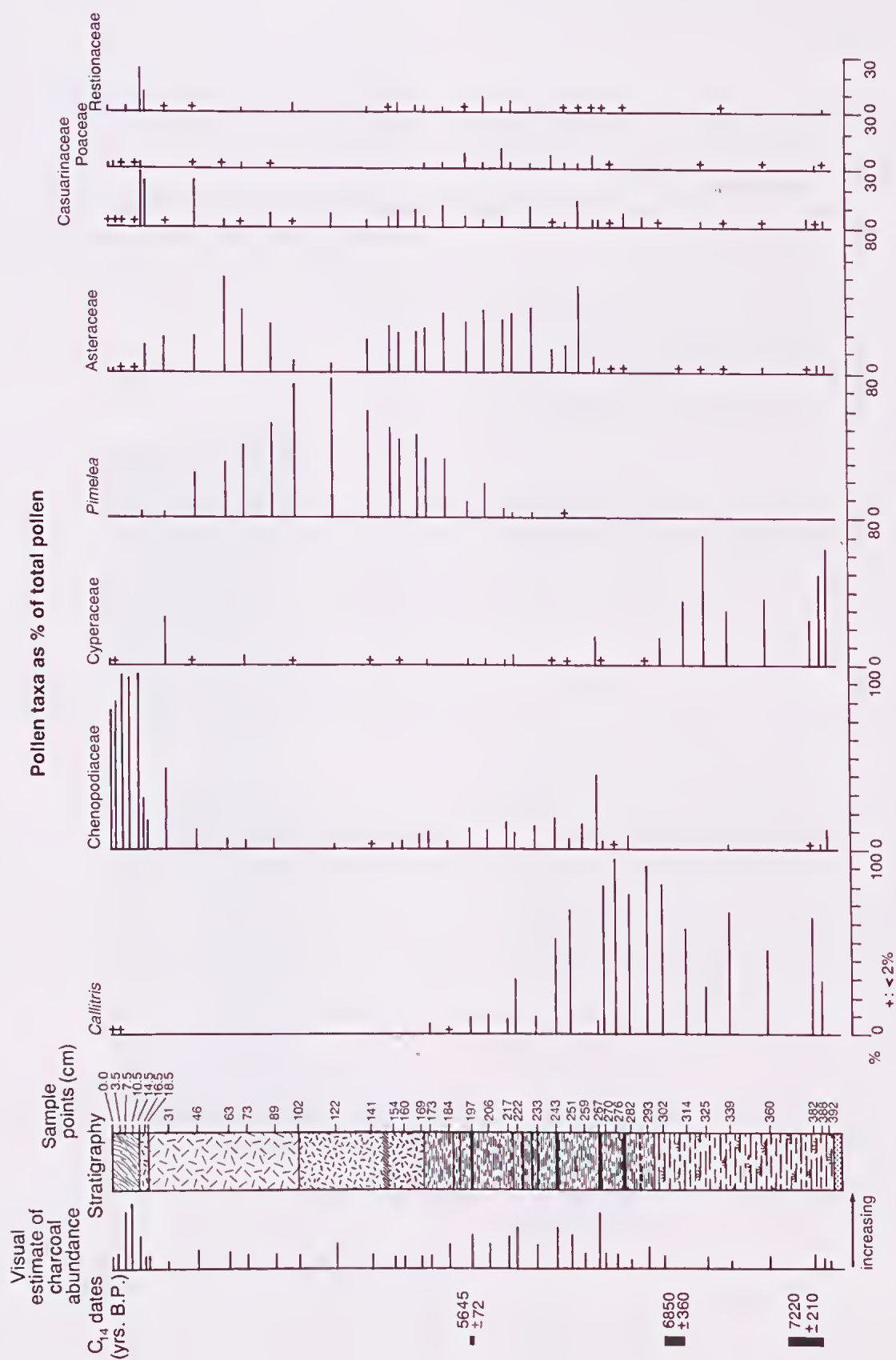
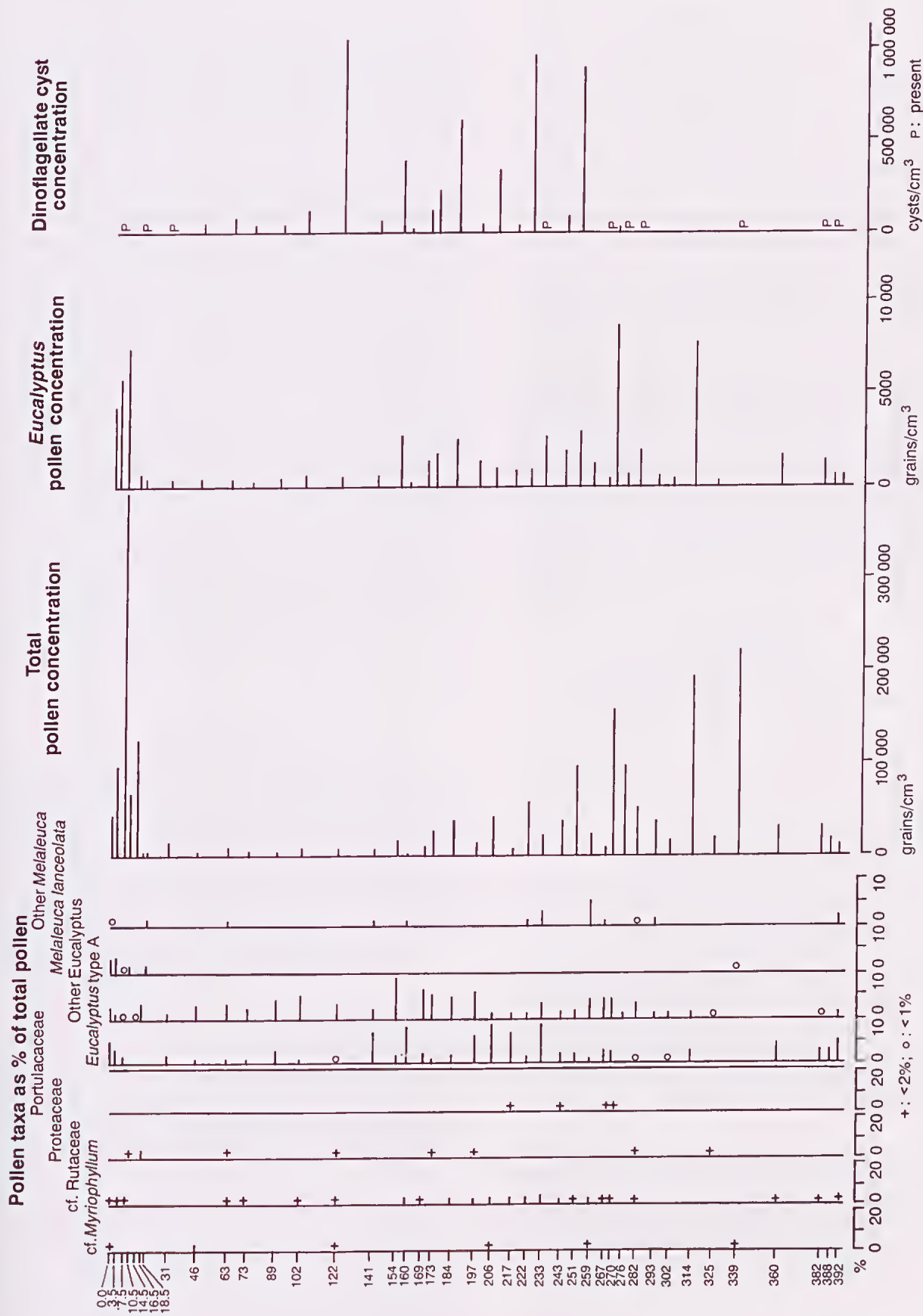


Figure 4. Barker Swamp 3: radiocarbon dates, charcoal abundance, stratigraphy, percentage pollen diagram, and pollen and dinoflagellate cyst concentration diagram. (cont. next page)



quokkas, except for food and water availability, may have led to greater grazing pressure, thus further restricting vegetation regrowth after fires.

During most of the Banded Calcilutite period the annual cycle of sedimentation in Barker Swamp consisted of deposition of a layer of algal material, probably in spring, followed by precipitation of calcium carbonate. In the periods following fires this pattern of sedimentation was disrupted. Instead of annual layering the sediments deposited during these periods consist of unlayered charcoal-rich bands, often followed by thicker layers of charcoal-rich, chocolate-brown calcilutite. The fires clearly affected sedimentation in the swamp for a period estimated to be at least 5 to 10 years, and possibly up to 40 years or more in some cases.

The 197 cm charcoal band is dated at 5645 ± 72 years B.P., which gives a sedimentation rate from the top of the Lower Peat to 197 cm of about 10 cm per 100 years. Assuming a uniform sedimentation rate for the whole of the Banded Calcilutite in Barker Swamp, deposition of this unit ceased approximately 5300 years B.P. This is within the period of sea-level high stand when much of the eastern part of Rottnest was inundated by the sea (Fairbridge 1958, Playford 1988).

In the succeeding Calcilutite interval, dinoflagellate cysts and subspherical algal cysts comprise much of the organic content. Plant debris and pollen are much less abundant, which suggests that the local vegetation was considerably sparser than in the preceding period. Darker bands with large quantities of charcoal have not been observed in the Calcilutite and it is concluded that fires became infrequent, or of much lower intensity, after about 5000 yrs B.P. The disappearance of fire-prone vegetation such as *Callitris* and *Eucalyptus* from the central-western part of the island is the most likely reason for this absence of significant fires.

The thin, cemented, hard band at a depth of 143 cm (estimated at about 4500 years B.P.) represents a period of severe desiccation, probably the result of a prolonged period of low precipitation. This is in agreement with Kendrick's (1977) record for reduced winter flows in the Swan River system during a mid Holocene dry period.

The hard band at 143 cm also marks the start of a period of extremely low rate of pollen deposition (Fig 4). Eucalypts were not regenerating in the area of Barker Swamp, and possibly nowhere on the island, at this time. This is also towards the end of the period of sea-level high-stand when the eastern part of Rottnest was inundated, with destruction of the remaining stands of eucalypts. Eucalypt pollen concentrations of fewer than 600 grains cm^3 of sediment between depths 14.5 and 141.0 cm in the Barker Swamp profile are interpreted as representing pollen blown from the mainland.

The absence of significant further changes in the pollen record through the Calcilutite indicates that conditions remained relatively arid through this period. From the pollen record, vegetation on the low ground around the swamp became dominated by *Pimelea*, with Asteraceae as the only other significant element of the flora.

The dominance of *Pimelea* and Asteraceae waned towards the end of the Calcilutite period. Chenopodiaceae, Cyperaceae, Restionaceae and *Casuarina* pollen all show patchy increases in relative abundance near the top of the

Calcilutite. This may indicate a slight increase in precipitation in the period immediately preceding European settlement, but the very low pollen concentration at this level precludes any firm conclusion on the cause of this change.

The record of *Casuarina* and *Pimelea* pollen is particularly interesting because neither are recorded from Rottnest as part of the original vegetation at the time of European settlement. *Pimelea* declined dramatically in the period immediately preceding settlement of the island, and is not observed in the pollen record above 16.5 cm, the highest sample representing pre-settlement conditions. Several factors may have caused its decline; amongst them grazing by quokkas and increased competition from chenopods, Cyperaceae and Restionaceae. Quokkas on Rottnest found *Pimelea* highly palatable when offered shoots brought from the mainland (*pers. obs.*). Grazing by domestic animals and more frequent fires after settlement possibly caused the final extinction of *Pimelea* on Rottnest. *Casuarina* is a major element in the pollen record at the top of the Calcilutite in an interval where the pollen concentration is extremely low. *Casuarinas* are wind pollinated and produce pollen in large quantities. It is possible that all or most of the *Casuarina* pollen in the Barker Swamp core was derived from the mainland. However, the frequency and consistency of *Casuarina* in the pollen record suggests that *Casuarina* was present on Rottnest in the past, and may have survived up to European settlement.

It is evident from the radiocarbon dates, and assuming continuous sedimentation, that the rate of accumulation of the Calcilutite interval was slower than the Lower Peat and Banded Calcilutite. If a date of 5300 years B.P. is accepted for the top of the Banded Calcilutite, and the change to buff-coloured calcilutite at 16 cm is taken as the start of European settlement in 1838, then the Calcilutite accumulated at a rate of approximately 3 cm per 100 yr.

The closely spaced samples at the top of the Barker Swamp section reveal the effects of European settlement. A sample of buff-coloured calcilutite from 14.5 cm contains considerably more charcoal than the immediately underlying sample at 16.5 cm. It also contains abundant chenopod pollen, but very few other pollen types. This sample is interpreted as representing the period of very early settlement when a small amount of burning and grazing had taken place. Charcoal is extremely abundant at 10.5 cm, and the pollen profile is essentially unchanged from the previous sample at 14.5 cm, except for a decline in the already low *Eucalyptus* count below detection levels. This represents a period of more intense fires on Rottnest, and the clearing of eucalypts on the mainland.

Reforestation on Rottnest started as early as 1886 (Sten 1959), but early efforts were largely unsuccessful. Major plantings of *Eucalyptus gomphocephala* started in 1932, and the large plantation at the western end of Serpentine Lake was planted between 1934 and 1944 (Sten 1959). The samples from 7.5, 3.5 cm and the surface show declining amounts of charcoal, still abundant chenopods, much higher concentrations of *Eucalyptus* and significant numbers of *Melaleuca lanceolata*. The two highest samples contain small numbers of *Callitris*, and pine pollen (not shown in Fig 4) comprises 0.5% of the pollen at 3.5 cm and 2% in the surface sample. The sharp increase in eucalypt pollen concentration in the 7.5 cm sample is the result of extensive eucalypt planting on Rottnest after 1932.

Despite the rather different sedimentary regimes, the eucalypt pollen concentration in the Surface Peat (0.0-7.5 cm samples) can be compared with the pollen concentration in the Banded Calcilutite and Lower Peat. On the available pollen evidence, eucalypts were no more common in the central part of the island 5000 to 7500 years ago than they are at the present day, although their distribution was probably different. An assessment of past eucalypt abundance on other parts of the island must await study of the pollen record from other sites.

Although *M. lanceolata* and *Callitris preissii* are known to have been quite common on the eastern part of the island at the time of European settlement (Pen & Green 1983), the pollen record suggests that *M. lanceolata* was a minor component of the vegetation in the vicinity of Barker Swamp until recent times. *C. preissii*, on the other hand, was once the dominant species, but it is not recorded in the pollen record between 7.5 and 169 cm. It is assumed that planting of *C. preissii* and *M. lanceolata* in areas near Barker Swamp has increased the number of pollen from these taxa in the Surface Peat.

The presence of *Acacia* pollen only in the surface sample accords with Churchill's (1960) recorded absence of *Acacia* pollen from the sediments of Lighthouse Swamp. *Acacia* polyads break down readily into undistinguished individual pollen. Isolated *Acacia* pollen were not observed in samples below the surface, despite careful examination of samples in the Surface Peat. It is concluded that *Acacia* was rare or absent in the past in the Barker Swamp area, and the presence of *Acacia* pollen in the surface sediments results from the recent introduction of *Acacia* to the area.

Conclusions

Comparison of cores from Barker and Salmon Swamps shows that the sequence of dark and light bands immediately overlying the Lower Peat is similar at both sites. By using this banding it may be possible to produce fine correlation between banded sediments from some or all of the swamps on Rottnest. If so, the same horizon could be sampled at several sites. Comparisons could then be made of the pollen flora and the microfauna between sites for coeval intervals, thus producing a series of palaeo-vegetation maps for the central-eastern part of the island.

This study did not replicate the results of Hassell & Kneebone (1960) at Lighthouse Swamp, partly because the vegetational history of Lighthouse Swamp is different from Barker Swamp. It is evident from Hassell's pollen diagram that chenopods are more significant at all levels in Lighthouse Swamp than at Barker Swamp, probably reflecting greater salinity caused by proximity to the sea.

The evidence from Barker Swamp partly supports the conclusion of Storr *et al.* (1959) and Churchill (1960) that a Tuart woodland or *Eucalyptus-Casuarina* woodland once existed on Rottnest. Evidence was found for the presence of *Eucalyptus marginata*, *E. gomphocephala* and other eucalypts, and occasional *Xanthorrhoea*, but the presence of other tuart woodland species was not confirmed. The tuart/jarraah woodland was not developed over the whole island. Dense stands of *Callitris preissii* occupied the area around Barker

Swamp for most of the period from 7500 to 5300 years B.P., and presumably this species was also dominant in other parts of the island.

This study suggests that similar detailed information can be obtained using pollen analysis, in conjunction with detailed sedimentological study, of Holocene intervals from swamps on the Swan Coastal Plain. However, because Barker Swamp is situated on an island and subject to considerable maritime influence it is not a typical coastal plain swamp. To some degree the sedimentary and pollen profile changes must reflect the severance of the land connection and increased maritime influence on the vegetation. Nevertheless, the aridity evident in the early period of Calcilutite deposition is probably the result of increased temperature and/or lower rainfall, factors not strongly influenced by minor changes in the proximity of the sea. Evidence from swamps on the mainland will be useful for further assessment of this mid-Holocene arid period.

Acknowledgements: Peter Thorpe of the Geological Survey of Western Australia provided conventional radiocarbon dates for two samples; the AMS date was provided by the Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand. Ostracod identifications and comments on known habitats were kindly provided by Patrick De Deckker of the Geology Department, The Australian National University. Molluscs were identified by George Kendrick of the West Australian Museum. Phil Ladd of Murdoch University provided considerable assistance to the project with the loan of equipment and with pollen identifications, and the study was suggested and encouraged by Dr. P.E. Playford, formerly Director, Geological Survey of Western Australia. The paper is published with the permission of the Director, Geological Survey of Western Australia.

References

- Churchill D 1960 Late Quaternary changes in the vegetation on Rottnest Island. *Western Australian Naturalist* 7:160-166.
- Edward D H D 1983 Inland waters of Rottnest Island. *Journal of the Royal Society of Western Australia* 66:41-47.
- Fægri K & Iversen J 1975 *Textbook of Pollen Analysis*. Munksgaard, Copenhagen.
- Fairbridge R W 1958 Dating the latest movements of the Quaternary sea level. *New York Academy Scientific Transactions Series* 2:471-482.
- Hassell C W & Kneebone E W S 1960 The geology of Rottnest Island. Honours thesis, Department of Geology, The University of Western Australia.
- Kendrick G W 1977 Middle Holocene marine molluscs from near Guildford, Western Australia, and evidence for climatic change. *Journal of the Royal Society of Western Australia* 59:97-104.
- Marchant N G & Abbott I 1981 Historical and recent observations of the flora of Garden Island, Western Australia. *Western Australian Herbarium Research Notes* 5:49-62.
- Moore P D & Webb J A 1978 *An Illustrated Guide to Pollen Analysis*. Hodder & Stoughton, London.
- Pen L J & Green J W 1983 Botanical exploration and vegetational changes on Rottnest Island. *Journal of the Royal Society of Western Australia* 66:20-24.
- Playford P E 1988 Guidebook to the geology of Rottnest Island. Geological Society of Australia, Western Australian Division Excursion Guidebook 2.
- Playford P E & Leech R E J 1977 Geology and hydrology of Rottnest Island. Geological Survey of Western Australia, Report 6.
- Sten T 1959 Rottnest Island Board. *Journal of the Royal Society of Western Australia* 42:91-192.
- Storr G M 1963 Some factors inducing change in the vegetation of Rottnest Island. *Western Australian Naturalist* 9:15-22.
- Storr G M, Green J W & Churchill D M 1959 The vegetation of Rottnest Island. *Journal of the Royal Society of Western Australia* 42:70-71.

Recent Advances in Science in Western Australia

Earth Sciences

The Pilbara coast, as described by V. Semeniuk, is dominated by active deltas, beach/dune shores, inactive eroding deltas and their barriers, limestone barriers and eroded limestone bays, and archipelagos. There are three main suites of Quaternary sediments, Pleistocene red siliciclastic sediments of the inland zone, local Pleistocene limestone barriers, and a Holocene system of deltas, beach/dunes, tidal flats and embayments.

Semeniuk V 1993 The Pilbara coast: a riverine coastal plain in a tropical arid setting, northwestern Australia. *Sedimentary Geology* 83:235-256.

The vegetation changes, described by J C Newsome of Murdoch University and E J Pickett of The University of Western Australia, for Boggy Lake during the last ca. 4500 years and at Lake McNess during the last ca. 9000 years cannot be attributed with certainty to climatic change. This is despite earlier claims of wetter mid-Holocene climates than at present, and an extensive arid phase in the mid to late Holocene.

Newsome J C & Pickett E J 1993 Palynology and palaeoclimatic implications of two Holocene sequences from southwestern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 101:245-261.

An international team of investigators from Curtin University, The University of Western Australia, Dalhousie University, the Geological Survey of WA, and the California Institute of Technology, describe each of the Abroholos platforms as consisting of a central platform of Last Interglacial reefs, about which windward and leeward Holocene reefs developed asymmetrically. In the Easter Group, windward Holocene reefs are 10 m thick and consist of a slow-growing association of coralline-algal bindstones and coral framestones, whereas leeward Holocene reefs are 26 m thick and dominated by fast-growing coral framestones.

Collins L B, Zhu Z R, Wyrwoll K-H, Hatcher G, Playford P E, Chen J H & Wasserburg G J 1993 Late Quaternary evolution of coral reefs on a cool-water carbonate platform: the Abroholos carbonate platforms, southwest Australia. *Marine Geology* 110:203-212.

D R Byrne and L B Harris, of the University of Western Australia, review Cu, Pb and Zn vein type deposits in the Northampton Complex, that occupy dilational sites along brittle-ductile shear zones formed during north-south dextral wrenching along the Darling Mobile Zone between 650 and 800 Ma.

Byrne D R & Harris L B 1993 Structural controls on the base-metal vein deposits of the Northampton Complex, Western Australia. *Ore Geology Reviews* 8:89-115.

Seismic data of B J Drummond and co-workers of the AGSO, Canberra, and C P Swager of the Geological Survey of WA, indicate that the greenstone belts of the Eastern Goldfields Province are shallow features 6-9 km thick superimposed on an otherwise uniform crust, and are not deep-rooted as is often supposed. The base is planar to subhorizontal, and appears to be block faulted in places.

Drummond B J, Goleby B R, Swager C P & Williams P R 1993 Constraints on Archaean crustal composition and structure provided by deep seismic sounding in the Yilgarn Block. *Ore Geology Reviews* 8:117-124.

Mineralisation in the Middle Vale Reef at Telfer is described by J P Vearncombe and A P Hill of the University of Western Australia to be coincident with the most deformed rocks in a strata-parallel shear zone in an argillaceous and calcareous horizon. This zone, which was a conduit for fluid during volume loss, reactivated with the addition of quartz-sulphide veins resulting in a net volume gain.

Vearncombe J R & Hill A P 1993 Strain and displacement in the Middle Vale Reef at Telfer, Western Australia. *Ore Geology Reviews* 8:189-202.

T Cruse, L B Harris and B Rasmussen of the University of Western Australia report the discovery of medusoid-like impressions and other possible biogenic markings of probable Ediacaran affinity in the Stirling Range. This suggests that the Stirling Range Formation was deposited between 590 to 540 Ma, which is less than half as old as previously thought, and folded during a late 'Pan-African' event common throughout adjacent parts of Gondwana but not previously recognised in southwestern Australia.

Cruse T, Harris L B & Rasmussen B 1993 The discovery of Ediacaran trace and body fossils in the Stirling Range Formation, Western Australia: Implications for sedimentation and deformation during the 'Pan-African' orogenic cycle. *Australian Journal of Earth Sciences* 40:293-296.

Life Sciences

A wide range of aspects of the biology of animals in the marine environment of Rottnest Island, WA, have recently been examined in a two volume series, edited by F E Wells (Western Australian Museum), D I Walker (The University of Western Australia), H Kirkman (CSIRO Marine Laboratories) and R Lethbridge (Murdoch University), that resulted from the Fifth International Marine Biological Workshop held at Rottnest Island in January 1991. Topics covered include the taxonomy and systematics of marine plants, mites, crustaceans, molluscs, echinoderms, and worms; ecology and behaviour; and physiology and functional morphology.

Wells F E, Walker D I, Kirkman H & Lethbridge R 1993 (eds) *The Marine Flora and Fauna of Rottnest Island, Western Australia*. Vols 1 & 2. Western Australian Museum, Perth.

N A M Verbeek and R Boasson of Simon Fraser University, in an examination of the leaves of rosette, climbing, and upright supporting sympatric *Drosera* sp in southwestern Australia, found that the catch per unit leaf was relatively constant regardless of growth form, but the height above ground of the capturing leaves influenced the terrestrial/aerial nature of invertebrate prey.

Verbeek N A M & Boasson R 1993 Relationship between types of prey captured and growth form in *Drosera* in southwestern Australia. *Australian Journal of Ecology* 18:203-207.

An assessment by R T Wills of the WA Herbarium for the ecological impact of the fungus *Phytophthora* in the Stirling Range National Park, Western Australia, showed that of the 330 species examined, some individuals of 36% of the species

had been killed by the fungus and 10% of the species were highly susceptible. Some plant families such as monocotyledons were not susceptible, but others such as Proteaceae were highly susceptible.

Wills R T 1993 The ecological impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. Australian Journal of Ecology 17:145-159.

Researchers from the Western Australian Wildlife Research Centre, CALM Woodvale, report from laboratory trials that the western quoll *Dasyurus geoffroii* consumes larger amounts of baits than expected, and discuss the susceptibility of western quolls to poisoned baits used in fox and dingo control. The preferred baiting season for least danger to western quolls is January to March.

Soderquist TR, Serena M 1993 Predicted susceptibility of *Dasyurus geoffroii* to canid baiting programmes: variation due to sex, season and bait type. Wildlife Research 20:287-296.

Recent research on seed germination of southwestern Australian species, which has been reviewed by D T Bell from the University of Western Australia and co-workers from ALCOA of Australia, shows that a range of environmental factors including temperature and light quality influence viability, dormancy and germination. Seeds time their germination to periods of the year and habitat conditions that are most conducive to seedling survival.

Bell DT, Plummer JA & Taylor SK 1993 Seed germination ecology in southwestern Western Australia. Botanical Review 59:25-74.

Bell DT 1993 The effect of light quality on the germination of eight species from sandy habitats in Western Australia. Australian Journal of Botany 41:321-326.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA).

Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. papers in refereed journals, or books, chapters and reviews will be accepted. Abstracts from conference proceedings will not be accepted. Please submit short (2-3 sentences) summaries of recent papers, together with a copy of the title, abstract and authors' names and addresses, to the Honorary Editor (c/o Western Australian Museum) or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc. Prof. G Hefter (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters, and suggest potential reviewers or respondents to your letter.

P C Withers, Hon Editor, Journal of the Royal Society of WA

Spread of the introduced yabby, *Cherax* sp (Crustacea: Decapoda: Parastacidae), beyond the natural range of freshwater crayfishes in Western Australia.

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Abstract

We report here on the presence of yabbies (*Cherax* sp, an exotic to Western Australia), in cave waters of an A Class Nature Reserve, near Eneabba, Western Australia. The geographic range of yabbies in Western Australia far exceeds that of freshwater crayfishes native to this State. It is argued that the spread of yabbies into natural waters beyond the distribution of native crayfishes is ecologically undesirable. However, the question of whether the spread of yabbies should be controlled has been applied only to their dispersion into waters containing native crayfishes.

Introduction

The natural distribution of freshwater crayfishes in Western Australia extends from the Hill River to the Kalgan River (Fig 1). This crayfish fauna comprises eight species in the genus *Cherax* [known in the vernacular as marron (*C. tenuimanus*), gilgies (*C. quinquecarinatus*, *C. crassimanus*, *C. glabrimanus*, and *C. neocarinatus*) and koonacs (*C. plebejus*, *C. preissii* and *C. glaber*)] and three species of *Engaewa* - strongly

burrowing crayfishes of very restricted distribution (*E. reducta*, *E. similis* and *E. subcoerulea*) from swamps near the coast between Dunsborough and Walpole (Riek 1967, 1969).

Yabbies (*Cherax destructor* and/or *C. albidus*) were introduced into Western Australia from Victoria in 1932, and spread by man throughout the southwest of the State (Morrissy & Cassells 1992). Austin (1985) first drew attention to the widespread occurrence of yabbies in this area, particularly in farm dams throughout the sheep and wheat farming districts. He classified yabbies as exotic to Western Australia, and raised the possibility that, should they spread from farm dams into natural habitats, they could displace marron (Austin 1985). Crayfish introductions to natural ecosystems can have many undesirable effects such as competition with native crayfishes, spread of disease, alteration of habitat through burrowing (Austin 1985) and co-introduction of symbionts, commensals, and parasites (Horwitz 1990).

Previous attention has focussed on the spread of yabbies into the southwest where their presence could be detrimental to the native crayfishes, especially marron (Morrissy & Cassells 1992). However, yabbies occur north of Perth, beyond the natural distribution of Western Australian endemic crayfishes, in natural waters including the Bowes and Hutt rivers, the Pilbara and hinterland of Carnarvon (Morrissy & Cassells 1992), and the Irwin and Chapman rivers (A Savage, pers comm). Despite this, no specific concerns have been expressed about the spread of yabbies in these northern areas.

We unexpectedly discovered yabbies (*Cherax destructor*) while sampling the streams of Aiyennu and Beekeepers caves near Eneabba (Fig 1) in June 1991. Both caves lie in Stockyard Gully Nature Reserve, an A Class Nature Reserve vested with the National Parks and Nature Conservation Authority for the conservation of flora and water, and pro-

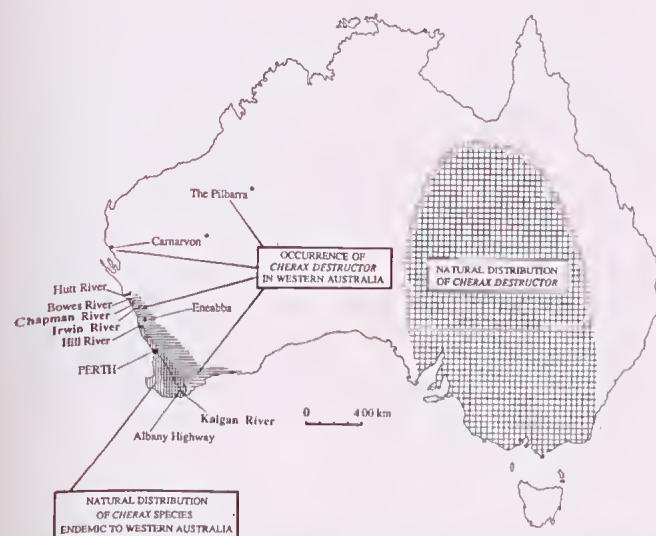


Figure 1. The natural distribution of freshwater crayfishes native to Western Australia, the known occurrence of the yabby (*Cherax destructor* and/or *C. albidus*) in Western Australia (a species exotic this State) and the natural distribution of the yabby in Australia. After: Austin (1986); Morrissy & Cassells (1992) and Riek (1969).

* mentioned in Morrissy & Cassells (1992) but the specific locations and range were not given.

tection of caves. We regard the spread of yabbies into a Nature Reserve as undesirable and raise here concerns over the spread of crayfish, and yabbies in particular, outside the natural distribution of crayfish in Western Australia.

Observations

Aiyennu (29°56'S 115°06'E) and Beekeepers caves (29°55'S 115°06'E), or E9 and E10 respectively after karst nomenclature (Matthews 1985), lie 21 km southwest of Eneabba within the Stockyard Gully Nature Reserve (# 36419 of 1406 ha). It is likely that the caves lie on the same stream in view of their similar physicochemistry (unpubl. obs.). Water depths varied between 0.5 m (Aiyennu) and 1.0 m (Beekeepers), but higher levels were clearly indicated by sediment horizons and chironomid larvae stranded on the banks of streams in both caves. No plant debris was observed within or about the water in either cave.

Invertebrates were abundant throughout the water column, with yabbies being the largest forms present. Composition of the aquatic fauna was similar in both caves and included oligochaetes, amphipods (*Austrochiltonia subtenuis*), copepods, dytiscid beetles, notonectid hemipterans, larvae of ceratopogonid, chironomid and stratiomyid dipterans. These invertebrates were the only obvious potential food source for the crayfish. In the accessible sections in each of Aiyennu and Beekeepers streams we observed about seven yabbies (ranging in size from about 5 cm to 15 cm total body length). These Eneabba specimens matched more closely the description of *Cherax destructor* than *albidus* (see Clark 1936).

Two yabbies from Aiyennu and four from Beekeepers cave were collected. These differed from surface crayfish in the lack of movement of eye pigments which remained constricted to the bases of ommatidia when tested with a range in intensity of illuminations using a halogen light source, and were slower in their normal locomotory movements and escape responses.

Speleological records

The trip reports of the two caving groups based in Perth typically record observations of cavernicoles. Hamilton-Smith (1965) noted the presence of a small aquatic snail in Aiyennu cave but made no mention of crayfish in any of the Eneabba caves. No yabbies were observed in the streams of either Aiyennu or Beekeepers caves during eleven trips reported between 1966 - 1984. There were no records of caving in either Aiyennu or Beekeepers from 1985 to 1988. Crayfish were first observed in Aiyennu in March 1989. These specimens were referred to as marron (Markey 1990) but since their identity was not confirmed (Markey, pers comm) we believe this name to be erroneous and instead presume the crayfish were yabbies.

Discussion

On the basis of the distributional data presented by Riek (1967, 1969) and the later report of Morrissy & Cassells (1992), it is reasonable to suggest that the freshwater faunas north of Hill River lacked crayfish before the recent introduction of yabbies. The effect of an exotic species of crayfish on the structure and composition of the fauna of local aquatic

ecosystems is an important issue which has been recognized elsewhere but not yet investigated here: "... once an 'exotic' crayfish is introduced into a lake or stream, it may impose considerable environmental stress on that system and, in all too many instances, irreparable shifts in species diversity occur" (Hobbs *et al.* 1989 p309). Spread of disease and displacement of native species through competition are discussed by Austin (1985) and Horwitz (1990). Yabbies are polytrophic, feeding on detritus, algae, live benthic and swimming invertebrates (Lake & Sokol 1986) and therefore have the potential to affect animals at various trophic levels. Their burrowing habits are likely to affect both the ecology of the benthos and water quality (Aller 1982). Therefore, it is important to assess urgently the impact of the introduction of yabbies into these northern river systems.

The recent presence of *C. destructor* in cave waters, about 40 km north of Hill River, highlights the spread of yabbies in Western Australia into areas beyond the natural range of crayfish. The presence of adult and juvenile crayfish in the two Stockyard Gully caves, together with their unusual eye and locomotory responses, suggest that the yabbies may now be established in the cave streams. We are unaware of the past or present distribution of yabbies in the wider Eneabba area, but Morrissy & Cassells (1992) report that yabbies were in Lake Logue before it dried up in 1986/1987. The Stockyard Gully karst does not support any surface waters but to the east, rivers and creeks flowing through private properties drain into the subterranean conduits of the Nature Reserve. In 1984, drainage from a neighbouring property into Stockyard Gully Cave was increased following excavation of the cave entrance (Jasinska *et al.* 1993). Hence, it is possible that yabbies entered the caves in waters draining the private properties east of Stockyard Gully Nature Reserve.

In a recent report on the spread of yabbies in Western Australia, Morrissy & Cassells (1992 p1) stated "In terms of both conservation issues and worthwhile additional production, any areal expansion of the present extensive harvesting of yabbies and, more especially, development of semi-intensive farming are best located in the warmer, near coastal, region north of Perth". Crayfish enter natural habitats either by escaping from dams and ponds (walking upstream or overland) or by human agencies. Therefore, until the impact of yabbies on ecosystems which do not contain an endemic crayfish fauna is ascertained, it would seem prudent to restrict crayfish farming to artificial ponds or tanks fitted with appropriate barriers to keep the crayfish from escaping, and to investigate ways in which dispersion of yabbies by humans into natural waters could be prevented.

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References

- Aller R C 1982 The effects of macrobenthos on chemical properties of marine sediment and overlying water. In: *Animal-Sediment Relations* (eds P L McCall & M J S Tevesz) Plenum Press, New York and London, 53-96.
- Austin C M 1985 Introduction of the yabbie, *Cherax destructor* (Decapoda: Parastacidae) into southwestern Australia. *Western Australian Naturalist* 16:78-82.

- Austin C M 1986 Electrophoretic and morphological systematic studies of the genus *Cherax* (Decapoda: Parastacidae) in Australia. PhD Thesis, University of Western Australia. 376pp.
- Clark E 1936 The freshwater and local crayfishes of Australia. Memoirs of the National Museum of Victoria 10:5-58.
- Hamilton-Smith E 1965 Some preliminary notes on Western Australian cave fauna. The Western Caver 5:1-5.
- Hobbs H H III, Jass J P and Hunter J V 1989 A review of global crayfish introductions with particular emphasis on two North American species (Decapoda, Cambaridae). Crustaceana 56:299-316.
- Horwitz P 1990 The translocation of freshwater crayfish in Australia: potential impact, the need for control and global relevance. Biological Conservation 54:291-305.
- Jasinska E J, Knott B & Poulter N 1993 The sanctity of caves in Stockyard Gully Nature Reserve, with comments on definitions of National Parks and Nature Reserves. In: Conference papers of TasTrog, 19th Biennial Conference. Australian Speleological Federation, Hobart, 25-31.
- Lake P S & Sokol A 1986 Ecology of the yabby *Cherax destructor* Clark (Crustacea: Decapoda: Parastacidae) and its potential as a sentinel animal for mercury and lead pollution. Australian Water Resources Council. Technical paper No. 87.
- Markey A 1990 Caving up north - Encabba (somewhere near Dongara). March 27-29th Easter Trip Report. The Western Caver 39:20-24.
- Matthews P G 1985 Australian Karst Index. Australian Speleological Federation Inc. Melbourne.
- Morrissy N M & Cassells G 1992 Spread of the introduced yabbie *Cherax albidus* Clark, 1936 in Western Australia. Fisheries Research Report, Fisheries Department of Western Australia 92:1-27.
- Riek E F 1967. The freshwater crayfish of Western Australia (Decapoda : Parastacidae) Australian Journal of Zoology 15:103-121.
- Riek E F 1969 The Australian freshwater crayfish (Crustacea : Decapoda : Parastacidae), with descriptions of new species. Australian Journal of Zoology 17:855-918.

Salinity trend of the Williams River, Western Australia

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Abstract

The Williams River has one of the highest stream salinity levels and one of the highest rates of salinity increase in southwest Western Australia. Temporal variation of stream salinity of the Williams River at Saddleback Road Bridge was examined by: 1) contrasting two periods with similar average flows; and 2) comparing trends in both salinity and stream flow for various periods. The contrast between flow-weighted average salinity for 1969-73 and for 1984-88 shows an increase of $51 \pm 0.7 \text{ mg L}^{-1} \text{ yr}^{-1}$, which is only 54 % of the previously published figure. The high rate of salinity increase previously documented is, to a large extent, a result of persistent low flows in the late 1970s. The 1980s have been a period of decreasing stream salinity as a consequence of increased flow. Variations in salinity are closely related to stream flow conditions. For the period of record (1967-90) the trend over time explains only 5.5 % of the variation in annual average salinity, whereas stream flow variation accounts for 74 % of the variation in salinity. The salinity trend is inversely related to that in stream flow. The effect of stream flow on salinity highlights the importance of long-term water quality monitoring.

Introduction

The Williams River catchment has an area of approximately 1,500 km², and lies 150 km south-east of Perth (Fig 1). The river flows westward, mostly through agricultural land. Roughly 90 % of the catchment has been cleared for grazing and cereal production (Public Works Dept. WA 1984). Mean annual rainfall is about 500 mm in the headwaters area and increases to about 800 mm near the Murray River confluence (Collins 1974). At Williams, which is located near the centre of the catchment, winter rainfall (June to August) constitutes more than half of the annual total and summer rainfall (December to February) constitutes no more than 10 % of the annual total.

The Williams River has one of the highest rates of increase in stream salinity ($95 \text{ mg L}^{-1} \text{ yr}^{-1}$ for the period 1966-86) in southwest Western Australia (Schofield *et al.* 1988, Schofield & Ruprecht 1989). With an average salinity of about 3,000 mg L⁻¹, the Williams River has been classified as brackish with little potential for future development as a source of domestic water supply (Schofield *et al.* 1988).

It is well known that an inverse relationship exists between the concentration of many stream solutes and stream flow because of the dilution effects of stream flow. For example, time series analysis of the salinity trend of the River Murray at Morgan (South Australia) showed a strong, inverse relationship between salinity and stream flow on a monthly basis (Cunningham & Morton 1983). In southwest Western Australia, a close relationship between stream flow and chloride load was reported for both cleared and un-cleared catchments (McPherson & Peck 1987). Therefore, the effect of stream flow must be evaluated before trends in solute concentrations can be assessed. In this paper, two approaches were used to evaluate stream salinity trends in the Williams River. First, we examined the salinity-stream flow relationship for two periods with similar stream flow conditions and the salinity increase for a given stream flow was determined. Secondly, trends in both salinity and stream flow were compared for different periods to identify the effect of stream flow on stream salinity.

Salinity data provided by the Water Authority of Western Australia were measurements of total soluble salts (TSS), in units of milligrams per litre (mg L⁻¹). Salinity was determined through ion analysis for 3.3% of the samples, the rest derived from electrical conductivity measurements (RDowd of WAWA, pers. comm.). In this paper, we use the terms salinity and TSS interchangeably.



Figure 1. Location map of the Williams River, Western Australia.

Contrasting Period Approach

To overcome fluctuations on small time scales, data for a certain period are sometimes aggregated to facilitate comparison with those in another period. For example, Pittock (1983) compared monthly rainfall for two contrasting periods (1913-45 versus 1946-78) to evaluate the likely change in rainfall due to the enhanced greenhouse effect. Likewise, Yu and Neil (1993a) contrasted rainfall total and high intensity rainfall for the periods 1911-50 and 1951-90 to establish the trends in southwest Western Australian rainfall.

A plot of the number of salinity samples per annum and annual stream flow of the Williams River at Saddleback Road Bridge (GS614196, catchment area = 1,437 km²) shows that 1975-80 is a period of intense salinity measurement and is also the period of lowest flow on record (Fig 2). Between July 1975 and November 1980, an average of 25 samples were taken per month in contrast to 1.6 and 1.8 samples per month for the periods May 1966 - June 1975 and December 1980 - September 1990, respectively. Average annual stream flow for the period 1976-80 was 20 mm, the lowest for any 5-year period in the 24 years of record (1967-90). The period 1975-80 likewise had the lowest stream flow for any 6-year period on record (23 mm). When choosing contrasting periods for the analysis of the Williams River salinity trend, we considered whether the two periods were well separated in time and whether the average stream flow and number of samples for the two periods contrasted were comparable.

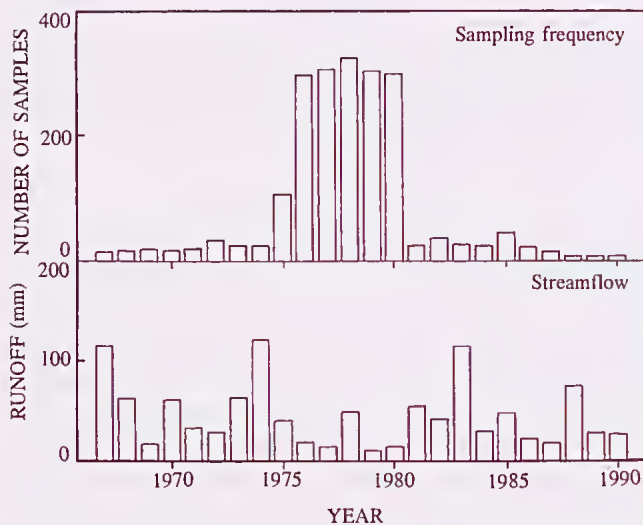


Figure 2. Salinity sampling frequency and annual stream flow at Saddleback Road Bridge (GS614196).

The periods 1969-73 and 1984-88 with a separation of 15 years (between mid-points) were chosen. Average annual stream flow for these two 5-year periods was 41 mm and 37 mm, respectively, in comparison with the long-term (24 years) average of 46 mm yr⁻¹. Furthermore, if more than one sample was taken on any given day, only the first sample was retained in the data set to ensure that samples were taken independently. As a result, a total of 28 measurements were discarded, and the number of samples for each of the two periods was 95 and 97, respectively. Three methods were

used to assess the salinity changes. 1) Rating curves for the two periods were compared. 2) Flow-weighted average concentrations for the two periods were compared. 3) The median test was used to estimate changes in median salinity values for the contrasted periods and for different flow conditions.

Salinity-stream flow relationship

As noted elsewhere (Yu & Neil 1993b) a simple log-linear model is inadequate to describe the relationship between salinity and stream flow in the Williams River. A second order term was introduced to fit the data, resulting in the following regression equations:

Period I (1969-73):

$$\log C = 3.6 - 0.22 \log Q - 0.084 (\log Q)^2, r^2 = 0.61; \quad (1)$$

Period II (1984-88):

$$\log C = 3.7 - 0.21 \log Q - 0.093 (\log Q)^2, r^2 = 0.73, \quad (2)$$

where C is TSS in mg L⁻¹ and Q is instantaneous stream flow in m³ s⁻¹. Standard errors of the estimate for the two regression equations are 0.016 and 0.07, respectively.

It can be seen from the scatter plot and fitted quadratic equations that maximum salinity occurs during intermediate flows for both periods analysed (Fig 3). To use these regression equations to estimate salinity for a given stream flow requires a bias correction factor due to the log-transformation (Ferguson 1986; Koch & Smillie 1986). Correction factors using the nonparametric method (Koch & Smillie 1986) for the two periods are 1.04 and 1.02, respectively. The rate of increase in salinity between the two periods varies in relation to stream flow (Fig 4). The rate of increase was standardised using its standard error (Fig 4) so that its value greater than 1.96 indicates a significant increase at 0.05 level. The maximum salinity increase of 69±18 mg L⁻¹ yr⁻¹ occurs for stream flow between 0.25 and 0.5 m³ s⁻¹. For stream flow of 0.01 m³ s⁻¹ the increase in salinity is 21±27 mg L⁻¹ yr⁻¹ and for stream flow of 10 m³ s⁻¹ the increase is 35±11 mg L⁻¹ yr⁻¹. For the average flow (1.8 m³ s⁻¹) the change in salinity is 57±1 mg L⁻¹ yr⁻¹.

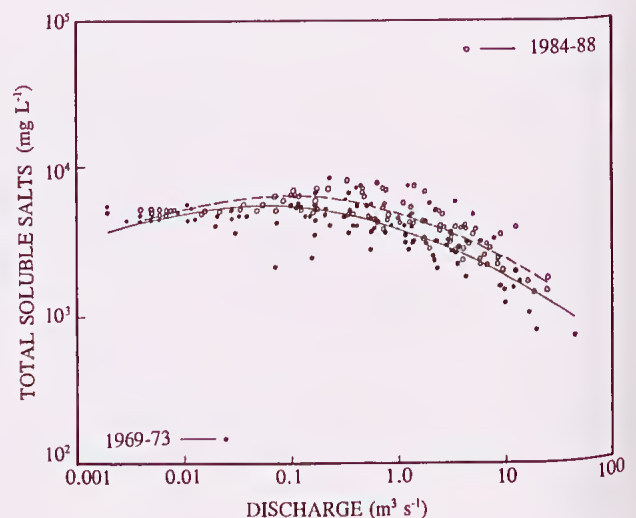


Figure 3. Comparison of salinity rating curves for the periods 1969-73 and 1984-88.

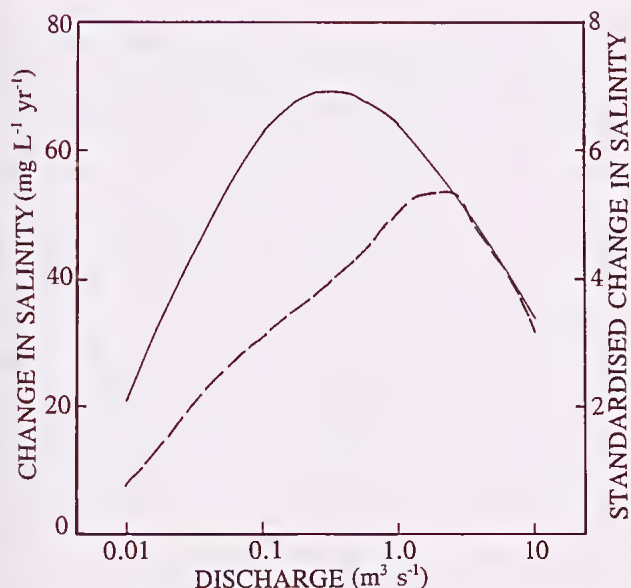


Figure 4. The rate of salinity increase (solid line) and the standardised rate of salinity increase (dashed line) between 1969-73 and 1984-88 in relation to stream flow.

Flow-weighted average salinity

Equations 1 and 2 were used as rating curves to calculate the total load for each of the two periods, respectively. Empirical rating curves, usually simple power functions, are commonly used to define the variation of concentration with stream flow in each transport mode (Richards 1982) and these rating curves have been widely used to calculate sediment loads of rivers (e.g. Walling 1977, Linsley *et al.* 1988). No systematic errors in salinity estimates were introduced by using average daily flows. Average salinity was estimated by dividing the total load for the two 5-year periods by the corresponding total stream flow volume. Assuming that daily salt loads are mutually independent, the variance of flow-weighted average salinity, C_{av} , is given by:

$$\text{Var}(C_{av}) = \frac{\sum Q_i^2 \text{Var}(C_i)}{(\sum Q_i)^2}$$

where Q_i represents daily flow, and C_i estimated daily TSS. Thus the standard error of the 5-year average salinity can be estimated using this relationship. The flow-weighted average salinity was $2,287 \pm 8 \text{ mg L}^{-1}$ for the first period and $3,055 \pm 6 \text{ mg L}^{-1}$ for the second period, which yields a significant average increase of $51 \pm 0.7 \text{ mg L}^{-1} \text{ yr}^{-1}$, or 34%, over the 15-year period.

Median test

Since water samples were effectively taken randomly, the median test (e.g. Gibbons 1971) may be used to determine whether the median TSS for the second period is significantly higher than that for the first period and to calculate the confidence interval for the difference in the median TSS. The test was performed on a common flow range (i.e. $0.0035 - 25 \text{ m}^3 \text{ s}^{-1}$) for both periods. Sample size within this range for the two periods is reduced to 91 and 97, respectively. Median salinity increased from $4,010 \text{ mg L}^{-1}$ for the first period to $4,710 \text{ mg L}^{-1}$ for the second period. Thus, the

median test showed an increase of $47 \text{ mg L}^{-1} \text{ yr}^{-1}$ with a confidence interval of -1.6 to $54 \text{ mg L}^{-1} \text{ yr}^{-1}$ (confidence level = 0.856) and such an increase was not significant at 0.1 level (p -value = 0.121).

Based on daily and instantaneous stream flow and salinity measurements for the two contrasting periods, we have shown that the salinity increase is likely to be in the range 47 – $57 \text{ mg L}^{-1} \text{ yr}^{-1}$. The lower and upper bounds of this range are based on the median test and on the rate of increase at average flow, respectively. $51 \pm 0.7 \text{ mg L}^{-1} \text{ yr}^{-1}$, based on the flow-weighted average, is the most reliable because the standard error of this estimate is lowest.

Varying Period Approach

To eliminate seasonal and other small-scale variations in stream salinity, annual flow-weighted salinity was estimated using the rating curve method. As noted in comparisons using the contrasting period approach, bias in the data set, due to an order of magnitude greater sampling frequency in the period 1975-80, should be removed before analysis. For this analysis, a bias-free sub-sample of the data set was obtained by extracting one observation per month from samples collected closest to the 1st of each month. This operation was repeated for the 15th and 30th of each month. Three separate rating curves ($n = 36$ for each) were then calculated for each of three year periods using each of these sub-samples. Flow-weighted salinity for each year of record was calculated from each of the three rating curves for each three year period. The annual flow-weighted salinity (Fig 5) used for ensuing analysis is an arithmetic mean of these three estimates. The average difference between annual salinity estimates, calculated from three sub-samples of the data set, is about 10 %.

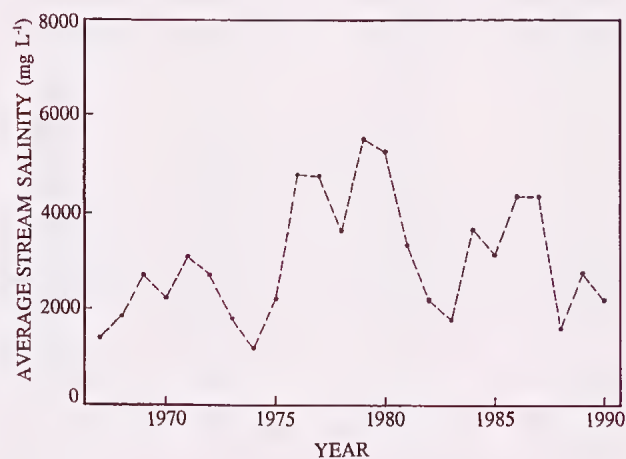


Figure 5. Time series of annual flow-weighted average salinity of the Williams River.

The long-term (1967-90) flow-weighted average salinity for the Williams River is $2,330 \text{ mg L}^{-1}$, varying from a minimum of $1,177 \text{ mg L}^{-1}$ in 1974 to a maximum of $5,493 \text{ mg L}^{-1}$ in 1979.

Standard statistical tests were applied to annual flow-weighted average salinity and stream flow to identify and

quantify stream salinity trends for varying periods of record. We used linear regression between concentration and time to determine the rate of change of salinity over time and Spearman's rank correlation coefficient to test for the occurrence of a trend in stream salinity (Table 1). The first part of Table 1 represents the conclusion regarding the trend in salinity which would have been reached at various times in the past, given commencement of salinity monitoring in 1967. The second part of the table represents the conclusion regarding salinity trend which would have been appropriate in 1990 if the monitoring program had begun at various

Table 1

Summary of salinity trends, their significance levels and correlation between salinity and stream flow for different periods.

r_s (C vs. T): Spearman's rank correlation coefficient between flow-weighted average salinity and time.

r_s (C vs. Q): Spearman's rank correlation coefficient between flow-weighted average salinity and stream flow.

* significant at 0.05 level ** significant at 0.01 level

Period	Rate of Change (mg L ⁻¹ yr ⁻¹)	r_s (C vs. T)	r_s (C vs. Q)
1967-76	142 ± 108	0.24	-0.89 **
1967-77	212 ± 97	0.42	-0.90 **
1967-78	202 ± 81 *	0.53	-0.84 **
1967-79	251 ± 74 **	0.63*	-0.87 **
1967-80	268 ± 64 **	0.70**	-0.90 **
1967-81	224 ± 61 **	0.70**	-0.86 **
1967-82	164 ± 64 *	0.54*	-0.84 **
1967-83	112 ± 64	0.34	-0.87 **
1967-84	106 ± 57	0.40	-0.87 **
1967-85	92 ± 51	0.42	-0.83 **
1967-86	98 ± 46 *	0.45*	-0.84 **
1967-87	101 ± 42 *	0.48*	-0.86 **
1967-88	70 ± 42	0.33	-0.88 **
1967-89	57 ± 39	0.32	-0.86 **
1967-90	42 ± 37	0.24	-0.83 **
1981-90	-23 ± 116	-0.05	-0.70 **
1980-90	-122 ± 110	-0.29	-0.77 **
1979-90	-185 ± 99	-0.45	-0.83 **
1978-90	-155 ± 85	-0.43	-0.77 **
1977-90	-163 ± 73 *	-0.52	-0.82 **
1976-90	-165 ± 63 *	-0.59*	-0.84 **
1975-90	-107 ± 65	-0.43	-0.82 **
1974-90	-45 ± 68	-0.19	-0.85 **
1973-90	-11 ± 63	-0.06	-0.87 **
1972-90	-1 ± 57	-0.01	-0.84 **
1971-90	1 ± 51	0.01	-0.82 **
1970-90	13 ± 47	0.04	-0.82 **
1969-90	17 ± 43	0.08	-0.77 **
1968-90	29 ± 39	0.15	-0.80 **
1967-90	42 ± 37	0.24	-0.83 **

times after 1967. Annual flow-weighted stream salinity has not changed significantly over the period 1967-90. Salinity trend varies considerably for different periods. For example, between 1967 and 1978-82, stream salinity increased significantly (at 0.05 level) and the maximum rate of increase was as high as 268 mg L⁻¹ yr⁻¹ (1967-80). In contrast, stream salinity has significantly decreased over time (again at 0.05 level) between 1976-77 and 1990 with a maximum rate of decrease of 165 mg L⁻¹ yr⁻¹ (1976-90). Inferences regarding trends in salinity are, therefore, strongly dependent on the sampling period in question.

Only 5.5% of variation in annual flow-weighted average salinity can be explained using the linear model to relate salinity to time for the period 1967-90. This is in stark contrast to 74% of variation in annual flow-weighted average salinity that can be explained by annual stream flow using a simple log-linear model for the same period. A plot of percentage of variation of annual salinity explained by annual flows against that explained by time for various periods (Fig 6) shows that a simple log-linear model using annual flows explains between 75 and 85 % of salinity variation for most periods; while a linear trend never explains more than 60% of salinity variation for any of the periods considered. Similarly, the rank correlation between salinity and time is less than 0.70 for all of the periods examined, whereas the correlation between salinity and stream flow is never less than 0.70 and it can be as high as 0.90 according to the time period considered. A significant correlation (at 0.05 level) exists between salinity and stream flow for all of the periods investigated (Table 1).

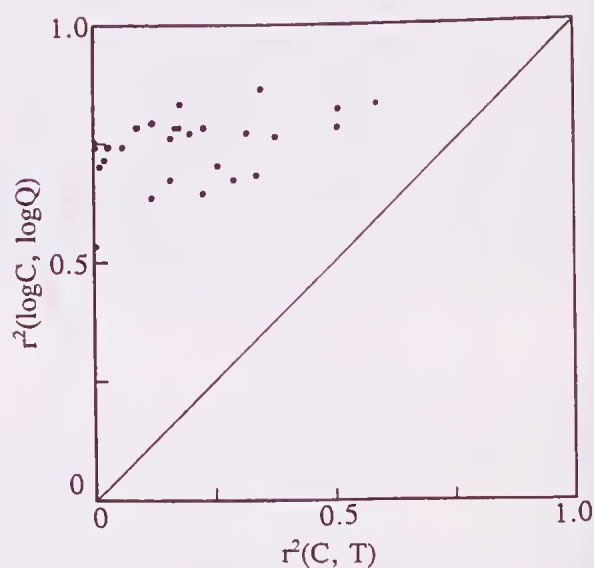


Figure 6. The relationship between percentage of salinity variation explained by a simple log-linear model based on annual flows and that explained by salinity trend.

With respect to trend in stream flow, annual stream flow significantly decreased (-4.3 ± 2.1 mm yr⁻¹; Spearman's r_s at 0.05 level) between 1967 and 1980 and no significant change in annual stream flow was detected for any other period. Changes in salinity and flow for various periods, expressed as a percentage of their respective long-term averages, are closely related (Fig 7). There is a clear inverse relationship

between change in stream flow and change in salinity when the change in salinity is significant. The inverse relationship between the trends in flow and salinity suggests that an increase in salinity is a likely result of a decrease in stream flow, *ceteris paribus*.

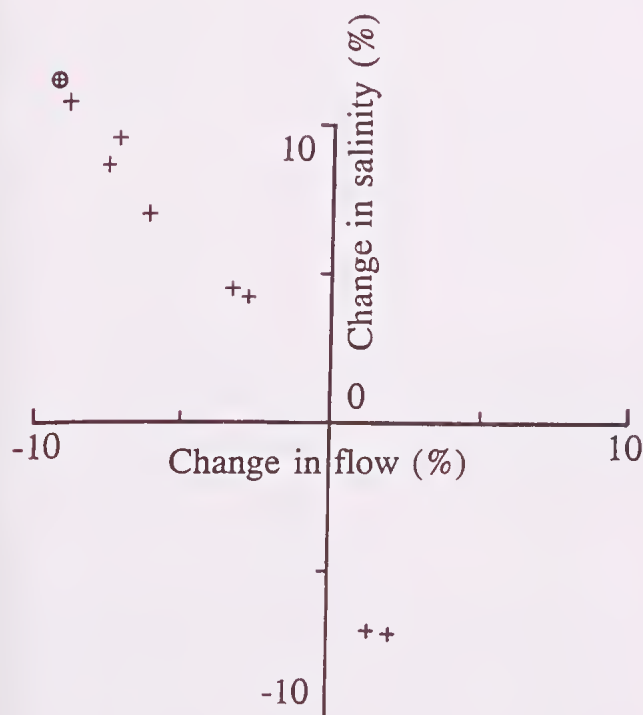


Figure 7. The relationship between trend in stream salinity and that in stream flow for various periods. Cross: only trend in salinity is statistically significant at 0.05 level; and cross and circle: trends in both salinity and flow are statistically significant at 0.05 level.

Examination of the temporal variation of salinity and stream flow for various periods thus shows that the inferred rate of change of stream salinity is highly sensitive to the period under consideration and is also strongly related to temporal variation of stream flow.

Discussion and Conclusion

Stream salinity is strongly correlated with stream flow, as demonstrated in both this and other studies. It follows that it is necessary to take account of both the variation and trend in stream flow when assessing salinity trend. In this study, several methods have been employed to estimate the change in stream salinity over the period 1967-90. The methods used, which take account of stream flow variation, yield quite consistent results, suggesting that the intrinsic change in salinity in the Williams River over the study period was an increase of about $50 \text{ mg L}^{-1} \text{ yr}^{-1}$. Although this rate of increase is significant in terms of water quality standards, it is about half of the rate previously documented for this stream.

In the light of the strong relationship between stream flow and salinity and the consequent temporal variation in salinity, a re-examination of documented salinity trends for other rivers in the region is necessary. The regionally consistent rainfall trend (Yu & Neil 1993a) suggests that a downward revision of the salinity trend in many streams is a likely outcome. Such a reassessment should be undertaken using more rigorous statistical procedures than previously and taking account of trends in stream flow.

The variable period approach used shows that the salinity trend over time is a relatively minor component of the variation in salinity, by far the most important factor being the stream flow. However, significant salinity trends, both increasing and decreasing, have occurred during some time periods. These results reinforce the necessity of placing analysis of all water quality time series in the context of changing environmental conditions. It is also clear that refinement of our understanding of salinity in an environment of high climatic variability and uncertain climatic trends requires the maintenance of long-term data series which permit a statistically rigorous separation of the different factors contributing to stream water quality.

In conclusion, it has been shown that salinity in the Williams River has increased significantly at about $50 \text{ mg L}^{-1} \text{ yr}^{-1}$ over the period of available records. This result constitutes a downward revision by about 50% of the rate previously documented. Stream salinity is largely related to stream flow in the Williams River, with 74 % of variation in stream salinity explained by stream flow variation in contrast to only 5.5 % of stream salinity variation being explained by the salinity trend.

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References

- Collins P D K 1974 Murray River Basin Surface Water Resources Survey. Public Works Department of Western Australia.
- Cunningham R B & Morton R 1983 A statistical method for the estimation of trend in salinity in the River Murray. *Australian Journal of Soil Research* 21: 123-32.
- Ferguson R I 1986 River loads underestimated by rating curves. *Water Resources Research* 22: 74-76.
- Gibbons J 1971 *Nonparametric Statistical Inference*. McGraw-Hill, New York.
- Koch R W & Smillie G M 1986 Comments on "River loads underestimated by rating curves" by Ferguson R I. *Water Resources Research* 22: 2121-2122.
- Linsley R K Jr, Kohler M A & Paulhus J L H 1988 *Hydrology for Engineers*. McGraw Hill, New York.
- McPherson D K & Peck A J 1987 Models of the effect of clearing on salt and water export from a small catchment. *Journal of Hydrology* 94: 163-179.
- Pittock A B 1983 Recent climatic change in Australia: Implications for a CO_2 -warmed earth. *Climatic Change* 5: 321-340.
- Public Works Department of WA 1984 *Streamflow Records of Western Australia to 1982 Vol 2 Basins* 613-617.
- Richards K 1982 *Rivers: Form and Process in Alluvial Channels*. Methuen, London.
- Schofield N J, Ruprecht J K & Loh I C 1988 The impact of agricultural development on the salinity of surface water resources of south-west Western Australia. Water Authority of Western Australia, Report No. WS 27, 69 p.

- Schofield N J & Ruprecht J K 1989 Regional analysis of stream salinisation in southwest Western Australia. *Journal of Hydrology* 112: 19-39.
- Walling DE 1977 Assessing the accuracy of suspended sediment rating curves for a small basin. *Water Resources Research* 13: 531-538.
- Yu B & Neil D T 1993a Long-term variations in regional rainfall in the southwest of Western Australia and the difference between average and high intensity rainfalls. *International Journal of Climatology* 13: 77-88.
- Yu B & Neil D T 1993b Temporal and spatial variations of the total dissolved solids, Williams River, Western Australia. In: Chowdhury R N & Sivakumar M (eds.) *Environmental Management, Geo-Water and Engineering Aspects*. A A Balkema, Rotterdam, 245-250.

Biogeographic significance of the Nullarbor cave mygalomorph spider *Troglodiplura* and its taxonomic affinities

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Abstract

Troglodiplura is now known from three widely separated, southern Nullarbor caves. Notes and illustrations are given of recently collected specimens. The distribution in relation to postulated earlier bioclimatic scenarios is discussed and notes on the biology given. A reassessment of the taxonomic position of *Troglodiplura lowryi* Main concludes that its affinities are with the Diplurinae as recently delimited. The genus has no recognisable close affinity with other known genera of Australian Mygalomorphae.

Introduction

The blind mygalomorph spider *Troglodiplura lowryi* Main was first described from Roach's Rest Cave near Madura, Western Australia (Main 1969). At the time, the spider was of considerable interest because it was one of only three troglobitic mygalomorphs known and the first described from Australia. There are now about 13 or 14 species of troglobitic mygalomorphs described (Gertsch 1971, 1973, 1982) but *Troglodiplura lowryi* Main remains the only known Australian species.

Although a fragmented, incomplete specimen of indeterminate sex, the Nullarbor specimen described in 1969 could be attributed readily to the subfamily Diplurinae (as then defined) of the Dipluridae. Subsequently Main & Gray (1985) described a male specimen from another cave (Cave 5N253 NNW of the Head of the Bight in South Australia). This was also a fragmented specimen and like the holotype the carapace was damaged and the abdomen missing. However the bipectinate tarsal claws and structure of the male sex characters e.g. pedipalp and a spur on the first tibia confirmed the earlier placement in the Diplurinae (as then defined). Main & Gray (1985) discussed the possible relationships of the species in this context but decided it had no close affinity with other Australian genera attributed to the Diplurinae at that time.

Two further male specimens of *Troglodiplura lowryi* have been collected from a third cave, Old Homestead Cave, north of Madura in Western Australia. Again fragmented and with the abdomens missing, these specimens nevertheless retain features which further add to our previous concept of the taxon. Descriptive notes are given, parts of the two specimens are figured and a photograph of a living specimen taken earlier is presented here.

More recently, M R Gray from the Australian Museum has collected several living juvenile specimens and the fragments of seven carcasses and/or castes from Cave 5N253.

One of the juveniles subsequently died and notes on it and the fragmented specimens are given here.

Troglodiplura is here redefined, its systematic position reassessed, hypotheses are proposed regarding its biogeographic origins and notes are given on its biology.

Methods

For the scanning electron microscopy, the specimen was taken from 70% alcohol, further dehydrated in absolute ethanol and super dried in a critical point dryer; the specimen was then mounted on a stub, gold coated and viewed with a Phillips 505 SEM using a modified Quentron backscatter detector.

A map is given here (Fig 1) showing the approximate locations of the caves from which *Troglodiplura* has been collected.

Abbreviations: AM, Australian Museum; SAM, South Australian Museum; WAM, Western Australian Museum. Measurements are in millimetres; spination in descriptions: v, ventral; d, dorsal; pv, prolatero ventral; rv, retrolatero ventral.

Systematic position and zoogeography of *Troglodiplura*

In his rearrangement of mygalomorph families and genera, Raven (1985) tentatively placed *Troglodiplura* in the newly elevated Nemesiidae into which family he transferred certain non-Australian genera and all those Australian genera (except *Kiama* Main and Mascord) previously included in the Diplurinae. However, he suggested at the same time that *Troglodiplura* might alternatively be "the only extra-Neotropical representative" of the Diplurinae (as he there defined the subfamily). Such a South American Gondwanan affinity was similarly suggested for *Troglodiplura* by Watson

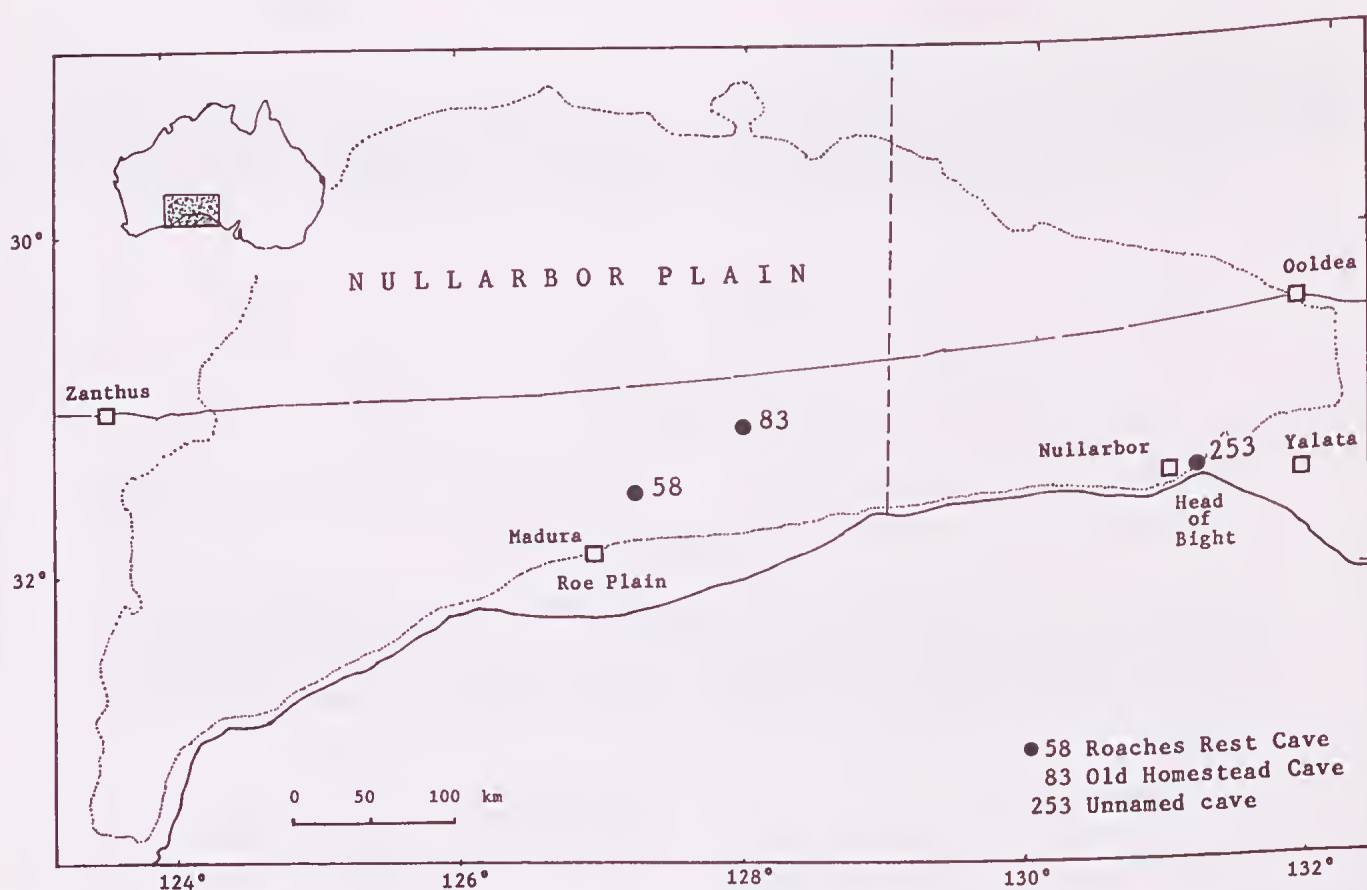


Figure 1. Map of Nullarbor Plain region and approximate location of caves from which *Troglodiplura* has been collected.

et al. (1990). The main definitive features of the Diplurinae noted by Raven (1985) are: bipectinate paired tarsal claws, a single row of cheliceral teeth, and pseudosegmented tarsi in males, "cracked" tarsi in females, and of course, the generalised characters of the family, primarily the low, flat, hirsute carapace and long posterior lateral spinnerets which distinguish diplurids from the Nemesiidae and Hexathelidae.

After further consideration of the Nullarbor specimens (and the photograph by Davey; Fig 2) and in the light of more recent examination of South American diplurines, I now suggest that *Troglodiplura* has closer affinity with *Diplura* Simon, *Liniothele* Karsch and *Trechona* Koch [as delimited by Raven (1985) and the only genera he includes in the Diplurinae *sensu stricta*] than with any of the other Australian genera I previously attributed to the Diplurinae (Main 1986) and of which most are now included in the Nemesiidae, except *Kiama* which has been transferred to the Cyrtoucheniidae (Raven 1985).

This postulated affinity is based on the following features: the antero-ental position of the maxillary cuspules and the elongated maxillary heel at least in the male (see Main & Gray 1985, their Fig 6), the "cracked" (Raven's term) tarsi *i.e.* prehensile or strongly arched tarsi (Figs 3 F, J and 4) with tangential lines indicating flexibility (Fig 4), the flat carapace (Figs 3 B, 5 B), and the simple elongate embolus (Fig 5 L-O) and subapical spined spur on tibia I of the male (Fig 3 D and 5 G, H) (see also Main & Gray 1985, their Figs 11-14). Paz & Raven (1990) figured distinctive pseudosegmentation in a female *Liniothele*. By comparison, the condition in *Troglodiplura*

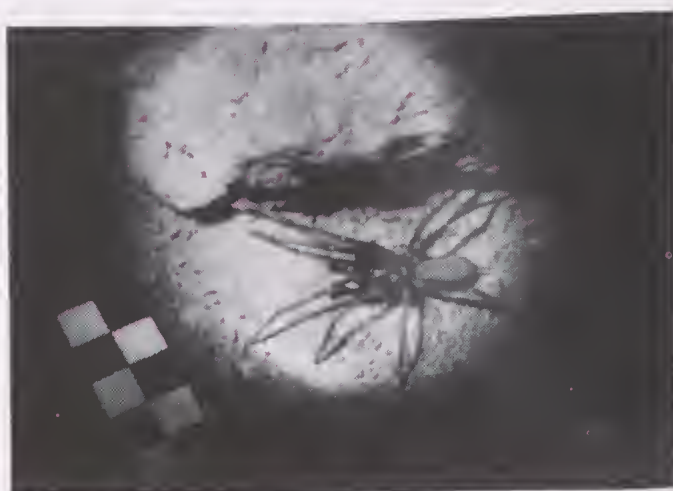


Figure 2. Photograph of torch-lit, live adult specimen of *Troglodiplura lowryi* in situ in Cave 5N 253 (photo by A D Davey, May 1982).

with fewer transverse lines or creases would be defined as "cracked" (see Fig 3, 4A, B) even though Raven (1985, p. 111) referred to it as "pseudosegmented". No adult specimen with intact abdomen has been collected but the photograph of a living specimen (Fig 2) and the juveniles collected by Gray clearly show the strongly arched tarsi (Fig 3 J) and flattened body form characteristic of the *Diplura* group of

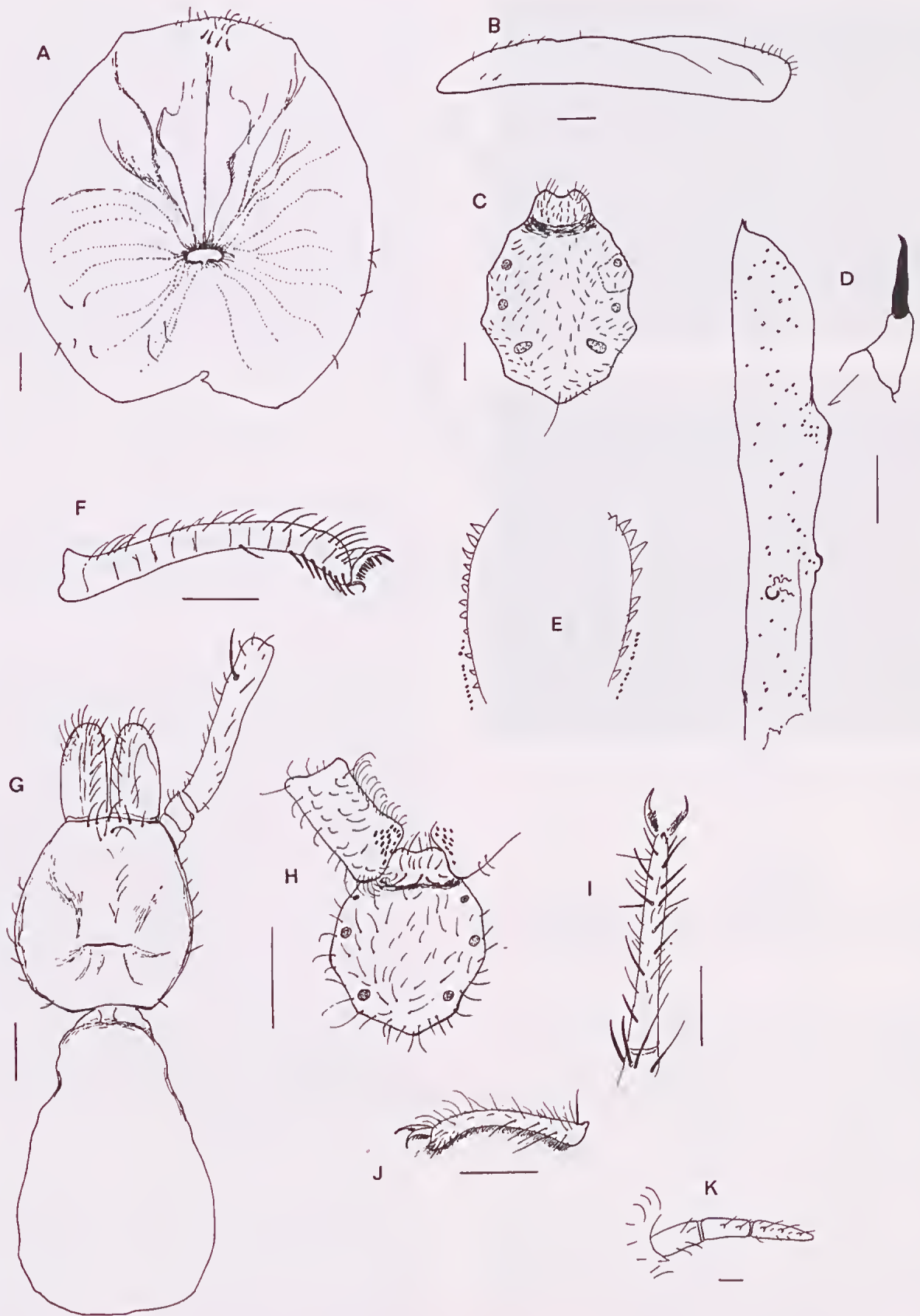


Figure 3. *Troglodiplura lowryi*. A-E, male specimen from Old Homestead Cave (WAM 91/255). A, dorsal view carapace; B, profile of carapace; C, sternum and labium; D, tibia I (right); E, cheliceral groove teeth, right and left chelicera respectively; F, tarsus of holotype; G-K, juvenile specimen (AM, KS30205); G, dorsal view specimen; H, sternum, labium and maxillae; I, tarsus IV ventral; J, right tarsus I; K, left posterior lateral spinneret.

Scale bars: A - D, F - J = 1.0mm; K = 2.0mm; E, not to scale.



Figure 4. A, B, holotype of *Troglodiplura lowryi*, SEM of tarsus showing faint "crack" lines indicating flexibility.

genera. However the spinnerets although tapering rather than rounded, and projecting well beyond the tip of the abdomen, are not as relatively long as in *Diplura* and related forms.

Nevertheless the general facies of the photographed and collected specimens is unlike that of Australian genera of Dipluridae e.g. Euagrinae, or Nemesiidae. Main & Gray (1985) noted some morphological similarities with *Stanwellia* Rainbow and *Pulleine* and other genera (now included in the Nemesiidae) e.g. the antero-ental position of the maxillary cuspules in *Stanwellia*, *Ixaniatus* Simon, *Xaniatus* Raven and *Auanie kirrauna* Raven [although the latter was originally stated by Raven (1984) to have antero-ental cuspules, Raven later (*in litt.*) noted that this species in fact has the typically widespread cuspule arrangement of *Ananie*]. However, of the foregoing only *Stanwellia* has the curved tarsi. In addition *Stanwellia* lacks tarsal spines on the female palp which combined with the flanged embolus suggests affinity with the South African nemesiid genus *Heruachia* Simon.

Although an affinity with nemesiids is unlikely (as discussed above), the taxonomic position of *Troglodiplura* nevertheless remains problematical as several morphological criteria still argue against a true diplurine affinity e.g. the relatively short posterior lateral spinnerets, the non-hirsute

carapace (although this could be expected because of the cavernicolous habit) and the position of the male tibial spined spur which is sub-apical not terminal on the segment.

Clearly the evolution of the nemesiid genera has been independent to that of the *Diplura*, *Liniotheke*, *Trechona* complex and possibly stems from an African element of a Gondwanan radiation rather than South American. If this is so, and if we accept a diplurine and thus South American affinity for *Troglodiplura*, then this genus is arguably more recent in its isolation in Australia than that of the nemesiid genera. Such a hypothesis further suggests a parallel zoogeographic occurrence of *Troglodiplura* with the Actinopodidae (*Actinopus* Perty and *Plesiolenia* Platnick and Shadab in South and Central America and *Missuleua* Walckenaer in Australia) (see Platnick & Shadab 1976; Goloboff & Platnick 1987; Main 1976 p.260 & 1991).

Systematics

Troglodiplura Main

Troglodiplura Main, 1969: 9. Type species by monotypy, *Troglodiplura lowryi* Main. Raven, 1981: 340. Main & Gray, 1985: 154. Main 1985: 39. Raven, 1985: 111.

Revised diagnosis

Eyes absent. Low, broad, almost flat carapace with sparse hairs. Fovea straight or pit-like. Sternum broad, sigilla small, away from margin. Labium broad, anteriorly indented. Maxillae with pronounced heel and antero-ental cuspules, no serrula. Chelicerae with large teeth on promargin only of groove but with basal or short proximal row of small granule-like teeth on retromargin. Paired tarsal claws with double row of teeth, median claw long, unarmed; tarsal claw of palp with promarginal line of teeth only. Tarsi curved (arched) and with indications of pseudosegmentation (*i.e.* "cracked"). At least some tarsi (fourth) ventrally with fine spines or spine-like bristles. Tarsal organ low. Trichobothrial base corrugiform on one half only of base (see Main & Gray 1985, their Fig 18). Spinnerets only moderately long (Figs 3 K and 4). Male tibia I with spur bearing a large single spine in distal third; several additional spines. Palpal organ of male with tapering embolus continuous with bulb (Fig 5 L-O). Tarsal lobes of male palp not markedly asymmetrical (Fig 5 J, K). Female internal genitalia unknown.

Comments

Raven (1985) made the following erroneous statements regarding *Troglodiplura*, counter to the original description by Main (1969) and features of the holotype; "Fovea unknown"; "Sternum unknown"; "Tarsi of females...". Main (1969), in her description of the holotype stated the fovea was "straight", and included figures and descriptions of it and the sternum (Main 1969, her Fig 1 A, B). Raven's statement regarding the tarsi of "females" is clearly in error unless his assessment (which would have been unfounded) of the holotype was that it was a female contrary to Main's assessment that it was of indeterminate sex. Raven (1985) was further inconsistent when he distinguished *Spelocleuiza* Gertsch from *Troglodiplura* by the "domed apical segment of



Figure 5. *Troglodiplura lowryi* male from Old Homestead Cave (SAM). A, dorsal view carapace; B, profile of carapace; C, sternum and labium; D, maxillae; E, F, cheliceral groove teeth promarginal aspect (E, left, F, right chelicera); G, tibia I (left ? leg); H, tibia I (right ? leg); I, a paired tarsal claw; J, K, palp tarsus (left ?) proventral and prolateral aspects; L-O, bulb and embolus (stigma) of palp; L, N, right ?, pro and retrolateral aspects; O, M, left ? pro- and retrolateral aspects.

Scale bars: 1.0mm; E, F, I not to scale.

the PLS" yet he stated (correctly) "spinnerets unknown" of *Troglodiplura*.

Troglodiplura lowryi Main

Troglodiplura lowryi Main, 1969: 9. Main & Gray, 1985: 156. Raven, 1985: 81, 111. [Catalogue references not included].

Comments

There is no marked difference in the male characters (palp, tibia I) of specimens from widely separated localities. Although there is no evidence based on known configurations of the caves of a present continuity this does not preclude possible (albeit unlikely) tenuous connections which would allow gene flow between populations. Alternatively the cave populations may have resulted from several independent entries of a former widely distributed albeit scattered epigeic species. In that selective pressures would have been very similar for all cavernicoles, any morphological and reproductive distinctiveness would have been minimal. Thus, based on present evidence, the three known populations represented from Roaches Rest, Old Homestead and Cave 5N 253 are assumed to comprise a single species. Nevertheless it is noteworthy that the Nullarbor troglobitic araneomorph *Tartarus*, which was formerly regarded as a monotypic genus, now has four species attributed to it (Gray 1992). Thus further study, including possibly genetic analyses may indicate several species of *Troglodiplura*.

Notes on additional specimens of *Troglodiplura lowryi*

(1) Male specimen, fragments. Old Homestead Cave (6N 83), Western Australia, [50 Metres past RDF point], 5 April, 1986, G Pilkington. SAM.

Fragments include an entire carapace and sternal area, both maxillae and chelicerae, tarsus of left (?) palp and bulb/embolus of both palps, leg fragments including tibia of both first legs and some tarsal claws (Fig 5 A-O). The carapace is low, slightly convex but without a "raised" caput, cuticle with reticulated pattern and almost hairless; length 12.00mm, width 10.8 and height 2.4 at fovea, 2.5 at mid caput; group of bristles at "ocular" area; fovea pit-like. Sternum length/width respectively 5.4/5.0, labium length/width 0.9/1.8, covered with dense fine bristles. Maxillae 4.6 long, with pronounced heel and about 45 small antero-ental cuspules. Chelicerae with large, irregular teeth on promargin, 10 (left), 9 (right) and granule-like intermediate basal teeth. Tibia I with large spine-bearing spur in apical third of segment and three spines. A damaged tarsal claw (Fig 5 I) with mid keel and 9 teeth in each row. Palpal organ with broad bulb, not distinctly demarcated from embolus which is "bent" and tapering. Palp tarsus with symmetrical terminal lobes.

(2) Fragments of male specimen. Old Homestead Cave, Western Australia, [6N 83, North Cave b/w RDF Stations "D" and "F" approximately 2 km into cave (in dark zone), Ref. No. 1290-21], 23 December 1990, A Clark. WAM 91/255.

Fragments comprise: carapace (Fig 3 A, B), sternum and labium (Fig 3 C), chelicerae (fangs detached) (Fig 3 E), 2 leg coxae (part), one first tibia (damaged), spur detached (Fig 3

D), genital-covering area of abdomen. Carapace length 11.1mm, width 10.6, height at fovea and front margin 1.7, at mid "caput" 1.9. Sternum length 6.0, width 5.2. Cheliceral teeth, promargin 12 (right), 10 (left), basal outer/intermediate 12 (right), 11 (left), extending to proximal third tooth on promargin.

(3) Juvenile collected alive, died subsequently. Cave 5N 253 Nullarbor Plain, South Australia, [Field no. 285], 11 July 1991, M R Gray. AM, KS 30205.

As this is the only complete specimen ever obtained it is described in detail although a juvenile. (Fig 3 G-K and Table 1).

Table 1.

Troglodiplura lowryi juvenile specimen (AM KS30205) leg measurements.

Leg formula = length of leg divided by carapace length. Tibial index = width of patella X 100 divided by length of tibia + patella (Petrunkevitch 1942).

Leg formula:	4	1	2	3		
	5.06	4.5	3.8	3.9		
	Femur	Pat	Tib	Mt	Ta	Total
I	4.0	1.9	3.7	3.2	2.1	14.9
II	3.5	1.4	2.9	3.4	1.5	12.7
III	3.3	1.2	3.0	3.6	1.9	13.0
IV	3.8	1.4	4.3	4.9	2.3	16.7
Palp	2.7	1.3	2.3	-	2.4	8.7
Width of patella I at knee = 0.5. Tibial index = 9.1						
Width of patella IV at knee = 0.5. Tibial index = 8.77						

Condition of specimen good although cuticle contracted and legs with some segments collapsed and folded stiffly under body. Pale tan colour, chelicerae darker than carapace and appendages, abdomen with integument pulled away from dorsum and spinnerets extruded as though specimen was about to moult. Carapace (Fig 3 G) length 3.3, width 3.0; with a line of bristles along anterior margin of carapace and a group of four bristles at "ocular area" (eyes absent). Fovea broad and straight. Cervical area slightly elevated. Sternum plus labium (Fig 3 H) length 1.8, width 1.5; uniformly cov-

ered with long fine bristles of even length. *Maxillae* with antero-ental cuspules extending along at least half length of inner edge, 20 (right maxilla) 23 (left, of which two are proximally isolated). *Sigilla* small, round, indistinct and close to the margin. *Chelicerae* long, projecting, no rastellum or apical spines; dorsally with longitudinal band of long bristles on inner edge; promargin of groove with 9 teeth, the two proximal teeth separated from others, retromargin 8 (left) 7 (right) basal teeth, retromarginal line extends to third proximal tooth of promargin. *Legs*. Dimensions (see Table 1). Tarsus I (Fig 3 J) and II distinctly curved, others less so (see Fig 3 I, tarsus IV). Tarsus of left palp slightly curved but possibly a shrinkage artefact. Fine ventral spines on tarsi III and IV, 7 or 8 on IV. Metatarsus III and IV with a comb-like apical pair of spines. *Scopula* complete on palp tarsus, tarsi and metatarsi I and II, sparse and incomplete on tarsus and metatarsus III and absent from leg IV. *Trichobothria* absent (?) from palp tarsus, one only on tibia; long and numerous on leg tarsi and metatarsi, longer on posterior than anterior legs (length up to 1.7 mm on metatarsus IV); about 12 in irregular line on tarsus I, few (3 or 4 plus some short trichobothria) on other legs, 11 to 15 on metatarsi and 12 to 15 (double row) on tibiae. *Spination* Palp-Tarsus 0, tibia v 3 apical 2 sub-apical. Leg I-Tarsus 0, metatarsus rv 1 median rd line of about 12 bristles above scopula, tibia rv 1 delicate spine in apical third, femur pd 1 apical. Leg II-Tarsus 0, metatarsus v pair proximal bristles. Leg III-Tarsus v about 15 delicate spines, metatarsus pv / rv 13 d apical pair, tibia pv / rv about 7 spine-like bristles, femur d 1 median. Leg IV-Tarsus v about 18 delicate spines, metatarsus pv / rv about 16 d apical pair, tibia pv / rv about 7 fine bristles and spines, femur d 1 median. *Tarsal claws*, palp with 5 promarginal teeth, tarsus IV with about 10 teeth in each row of both paired claws, inner rows more distal than outer rows. *Spinnerets* not excessively long, much shorter than abdomen and with few spigots (Fig 3 K); dimensions of posterior lateral spinnerets, basal segment 0.5, median 0.4, terminal 0.6.

Seven additional specimens (listed below) were collected dead from the same cave as Specimen (3), all were fragmented and none was complete.

(4) Fragments of carcase, female. Same data as for specimen (3), M R Gray field note 2851. (AM).

Carapace low, length 11.36, width 9.9. Deep straight fovea. Sternum length 4.9, width 4.5. *Chelicerae* with 9 (right), 10 (left) retromarginal teeth of irregular size. Several leg fragments, one tarsus (IV ?) with fine spines, some tarsi and metatarsi with dense scopulae.

Specimens (5) to (10) same data as (4).

(5) MRG 2853. (AM). Slightly smaller specimen. Cheliceral teeth, 9 (right); scopula on tarsi.

(6) MRG 2858 (AM). Crumpled pieces in a "bolas", possibly a cast skin. Cheliceral teeth 9 (left); scopula on tarsi.

(7) MRG 2857 (AM). Slightly smaller than (4). Cheliceral teeth 9 (right and left).

(8) MRG 2855 (AM). Pulverised fragments.

(9) MRG 2856 (AM). Pulverised fragments, possibly a cast, one curled tarsus identifiable.

(10) MRG 2854 (AM). Male, pulverised fragments, tibia of a first leg identifiable, length 12.7, spined spur in apical third.

Discussion

All specimens collected have been found on the floor of caves. Numerous carcasses were reported by A Clark (*pers. comm.*), the collector of one specimen, to be in Old Homestead Cave. It is not known whether the spiders make a burrow and/or sheet web. However, if the affinity of *Troglodiplura* is correctly postulated as being with the Diplurinae (as now delimited by Raven (1985)) and as inferred by Raven (1985), and Watson *et al.* (1990) *e.g.* "probably belongs to a group of primitive web-weaving genera otherwise found only in South America", then the spiders would be expected to build a sheetweb with possibly a tubular retreat extending back into crevices or a shallow burrow in soil or debris. If indeed webs are sited in crevices, they could have escaped detection by speleologists or have been dismissed as webs of Araneomorphae *e.g.* *Tartarus* Gray, which is known to occur in many Nullarbor caves. Alternatively the spiders could simply spread a film or mesh on the substrate which would be enough to entrap crawling insect prey. The strongly curled anterior tarsi could be used either to probe on the bare substrate or pluck a flimsy sheet in either case then they could be somewhat analogous to the prehensile claws of the *Gradungulidae* which includes wandering and web weaving species. A reduced web or absence of such could account for the associated "atrophied" or shortened spinnerets.

Observations by M R Gray (*pers. comm.*) on specimens in captivity (specimens from Cave 5N 253) suggest that no web is made. Gray also observed spiders grasp and bite prey which they encountered while slowly wandering. Similarly spiders *in situ* (Cave 5N 253) were found either under rocks or wandering on the cave floor.

Gray also observed carcasses (and collected fragments of seven) which may have been washed together near a wall of the cave. Gray noted that the cave was energy rich and wet (*pers. comm.*).

The 5N 253 cave system may receive drainage from the Yalata Swamp area to the east. This vast low-lying area of saucer-like depressions, with shrubby chenopodaceous plants, fills intermittently with fresh water. I have collected flood-adapted nemesiid spiders in the area. The whole area *i.e.* Head of the Bight is also subjected to onshore fogs throughout the year including during the summer. That neither of the Western Australian caves have yielded living material is possibly due to progressive drying of the climate with added desiccation due to their greater distance from the coast and thus less surface precipitation and moisture currently draining into the caves.

Presumably ancestors of the spiders originally lived in wet shaded situations amongst vegetation on the surface, firstly (Pre-Miocene) to the north of what is now the Nullarbor Plain and later either on the Plain itself or the northern

boundaries. There is ample evidence of an early-mid Tertiary humid climate prevailing in the Nullarbor region which supported a *Nothofagus*-associated rainforest vegetation, particularly *Phyllocladus*-type representatives. Fossil plant deposits (Cookson 1953, Cookson & Pike 1953, 1954) imply a cool-temperate rainforest type of vegetation across southern Australia and penetrating to the Alice Springs region. Grodzicki (1985) argued that a humid climate was responsible for the karst formations of caves in the Nullarbor and postulated that a subsequent arid climate has been responsible for preservation of the caves while simultaneously causing the peneplanation of the region and erasing the surface drainage pattern which would have been connected to the subterranean system. Nevertheless palaeodrainage lines are still recognisable on the northwestern boundary of the Nullarbor (van de Graaff *et al.* 1977). These drainage lines are interpreted as relics of Cretaceous rivers. Following formation of the "plain" patches of former "rain forest" associated with the terminal sinks of the old rivers (the precursors of the present drainage pattern in which dolines and solution channels have probably formed) could have been scattered across the "plain" and also as "gallery" forests along the northern headwaters of the old drainage courses.

At such a time the archetypal *Trogloidiplura* probably made sheet webs amongst the tree buttresses, exposed roots, stones and debris around the butts of trees and rock tumbles. With a drying of the climate, gradual recession of the forest and retreat of water from underground channels formed by earlier percolation beneath a wet forest floor, the spiders could have gradually followed a sequence of habitats from forest floor to cavern-like, semi-epigean nooks in tree buttresses and hollows, retracting finally into deep caves as the surface became completely arid.

Deeleman-Reinhold (1978) in her discussion of the ecology of Linyphiidae in Yugoslavian caves described what had earlier been termed the "microcavernicole" habitat (Racovitza 1907, cited in Deeleman-Reinhold 1978) as a kind of continuum from the forest floor under *Fagus* and other trees to underlying caves common there in limestone. This microcavernicole habitat comprised a network of channels formed by small burrowing mammals in the deep humus and moss of the forest floor. One can imagine a similar scenario on the "Nullarbor" or along its northern boundary during the mid Tertiary when the wetter climate maintained a forest. Lacunae would form naturally in humus and debris by natural decay facilitated by fungi and possibly burrowing reptiles, certainly by invertebrates such as cockroaches, carab beetles, myriapods, orthopterans and spiders (all taxa now represented in caves).

One might query why today there are no known epigean representatives of the Diplurinae in Australia. In south eastern and eastern Australia and Tasmania the Hexathelidae generally fill the same niche and construct sheet webs analogous to those of the Diplurinae of South and Central America. In other parts of Australia the Euagrinae with their curtain webs are role equivalents. Nevertheless such similarity of behaviour and web construction does not completely explain apparent absence of Diplurines. The simplest explanation is that many present forest regions where they might still be expected to occur *e.g.* Tasmania, were subjected to Pleistocene glaciation. However there is a possibility that relic populations may occur in the northwestern corner

(Smithton region) of Tasmania. The Pleistocene climate was not so severe in this area and it was not subjected to glaciation (Colhoun *et al.* 1982). The Pleistocene ice cap was confined to the central mountains and the periglacial area although extending to mid-western Tasmania did not affect the north western region. Certain burrowing mygalomorphs on mainland Australia overwinter under the snow on mountain tops *e.g.* Brindabella Ranges in the A C T, Mt Baw Baw and Donna Buang in Victoria (Main 1976, pp. 227-228) so low temperatures as such need not preclude occurrence of spiders. Secondly, suitable rock exposures occur *e.g.* laminated surfaces of weathered sedimentary rocks for crevice-dwelling web weavers, albeit known to harbour hexathelines (pers. obs.). Even the extreme southwest of Western Australia may harbour relic representatives in suitable sites. Possibly those areas near Denmark where bore samples have revealed early Tertiary floral components (Cookson 1953; Cookson & Pike 1953, 1954) and Nornalup are worthy of further intensive investigation. If (as with several other typically southeastern Australian mygalomorph genera *e.g.* *Stanwellia* (Main 1990 p. 275)) the spiders are reduced in size where they occur in the less than optimal habitats, then they may have been overlooked in the relatively less mesic southwest forests. Thus these two regions are postulated as the "predictive" areas of occurrence for surviving epigean representatives of the Diplurinae. Only continued searching will test the validity of such biogeographic hypotheses.

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References

- Colhoun E A, van de Geer G & Mook W G 1982 Stratigraphy, pollen analysis and palaeoclimatic interpretation of Pulbeena Swamp, northwestern Tasmania. *Quaternary Research* 18: 108-126.
- Cookson I C 1953 The identification of the sporomorph *Phyllocladites* with *Dacrydium* and its distribution in southern Tertiary deposits. *Australian Journal of Botany* 1: 64-70.
- Cookson I C & Pike K M 1953 The Tertiary occurrence and distribution of *Podocarpus* (Section *Dacrycarpus*) in Australia and Tasmania. *Australian Journal of Botany* 1: 71-82.
- Cookson I C & Pike K M 1954 The fossil occurrence of *Phyllocladus* and two other Podocarpaceous types in Australia. *Australian Journal of Botany* 2: 60-88.
- Deeleman-Reinhold C L 1978 Revision of the cave-dwelling and related spiders of the genus *Troglohyphantes* Joseph (Linyphiidae) with special reference to the Yugoslav species. *Academia Scientiarum et Artium Slovenica. Classis IV: Historia Naturalis*. 23: 1-221.
- Gertsch W J 1971 A report on some Mexican cave spiders. *Association for Mexican Cave Studies, Bulletin* 4: 47-111.
- Gertsch W J 1973 A report on cave spiders from Mexico and Central America. *Association for Mexican Cave Studies, Bulletin* 5: 141-163.
- Gertsch W J 1982 The troglobitic mygalomorphs of the Americas (Arachnida, Araneae). *Association for Mexican Cave Studies, Bulletin* 8: 79-94.
- Goloboff P A & Platnick N I 1987 A review of the Chilean spiders of the superfamily Migoidea (Araneae, Mygalomorphae). *American Museum Novitates* 2888: 1-15.
- Gray M R 1992 The troglobitic spider genus *Tartarus* Gray with a cladistic analysis of *Tartarus* and *Baiaia* Lehtinen (Araneae: Stiphidiidae). *Proceedings of the Linnean Society of New South Wales* 113: 166-173.

- Grodzicki J 1985 Genesis of the Nullarbor Plain caves in southern Australia. *Zeitschrift Geomorphologie* N F 29: 37-49.
- Main B Y 1969 A blind mygalomorph spider from a Nullarbor Plain cave. *Journal of the Royal Society of Western Australia* 52: 9-11.
- Main B Y 1976 *Spiders*. Collins, Sydney.
- Main B Y 1985 Mygalomorphae. In: *Zoological Catalogue of Australia* Vol. 3 (ed D W Walton). Australian Government Publishing Service, Canberra, 1-48.
- Main B Y 1986 Further studies on the systematics of Australian Diplurinae (Araneae: Mygalomorphae: Dipluridae): A new genus from South-western Australia. *Records of the Western Australian Museum* 12: 395-402.
- Main B Y 1990 Dwarf males in mygalomorph spiders: adaptation to environmental hazards. *Acta Zoologica Fennica* 190: 273-278.
- Main B Y 1991 Occurrence of the trapdoor spider genus *Moggridgea* in Australia with descriptions of two new species (Araneae: Mygalomorphae: Migidae). *Journal of Natural History (London)* 25: 383-397.
- Main B Y and Gray M R G 1985 Further studies on the systematics of Australian Diplurinae (Chelicerata: Mygalomorphae: Dipluridae): Description of the male of *Troglodiplura lowryi*, with notes on its affinities. *Psyche* 92: 151-162.
- Paz N S & Raven R J 1990 A new species of *Linothele* from Colombia (Araneae, Mygalomorphae, Dipluridae). *The Journal of Arachnology* 18: 79-86.
- Petrunkovitch A 1942 A study of amber spiders. *Transactions of the Connecticut Academy of Arts and Sciences* 34: 119-464.
- Platnick N I & Shadab M U 1976 A revision of the mygalomorph spider genus *Neocteniza* (Araneae, Actinopodidae). *American Museum Novitates* 2603: 1-19.
- Raven R J 1981 A review of the Australian genera of the mygalomorph spider subfamily Diplurinae (Dipluridae: Chelicerata). *Australian Journal of Zoology* 29: 321-363.
- Raven R J 1984 A new diplurid genus from Eastern Australia and a related species (Diplurinae: Dipluridae: Araneae). *Australian Journal of Zoology Supplementary Series* No. 96: 1-51.
- Raven R J 1985 The spider infraorder Mygalomorphae (Araneae): cladistics and systematics. *Bulletin of the American Museum of Natural History* 182: 1-180.
- Truswell E 1990 A curious and diverse flora. In: *The Australian Environment: Taking Stock Looking Ahead: Proceedings of the 1988 National Conference*, Sydney (ed S Neville). Australian Conservation Foundation, Fitzroy, Victoria, 25-31.
- vande Graaff W J E, Crowe R W A, Bunting J A & Jackson M J 1977 Relict early Cainozoic drainages in arid Western Australia. *Zeitschrift für Geomorphologie* N F 21: 379-400.
- Watson J, York-Main B & Humphreys B 1990 Living limestone. *Landscape* 5 (2): 28-34.



THE ROYAL SOCIETY OF WESTERN AUSTRALIA INCORPORATED

Constitution and Rules and Regulations

Constitution

1. The scientific society known as "The Royal Society of Western Australia Incorporated" (hereinafter referred to as "The Society") has the objects, purposes and powers hereinafter mentioned.
2. To promote and assist in the advancement of science.
3. To print and publish, or join in printing and publishing, one or more journals, periodicals, books, newsletters or other documents relating to science.
4. To promote, produce and hold, or join in promoting, producing and holding meetings, lectures and exhibitions in furtherance of any objects of The Society.
5. To found, subsidize or contribute to, for the benefit of any institutions or persons, scholarships, grants, prizes, or monetary or other rewards in connection with all or any of the objects or purposes of The Society.
6. To acquire by purchase, lease, exchange, hire, or by way of loan or otherwise, any real or personal property in furtherance of any objects of The Society.
7. To invest, sell, lease, hire, mortgage, charge, lend, surrender or otherwise dispose of, or deal with all or any part of the assets or property, real or personal, of The Society, or to borrow money and grant security therefor and to liquidate, redeem or discharge any obligations undertaken in furtherance of any objects of The Society.
8. To improve, develop or extend all or any of the property or rights of The Society, also to build, erect or alter any buildings or erections, and to furnish, fit up, and maintain the same and provide fittings, equipment and appliances.
9. To amalgamate, co-operate or affiliate with any other society, association or body having objects wholly or in part similar to those of this Society.
10. To protect or assist in protecting the interests or rights of any member or members of The Society.

Objects, purposes and powers

Rules and Regulations

Membership

11. The Society shall consist of members divided into the classes hereinafter mentioned, and the members who are, have been or may be duly elected as members of such respective classes shall have the rights and privileges hereinafter specified as appertaining to such respective classes, subject always to the due and punctual payment of the annual subscription or other sum hereinafter provided to be paid by the respective members of each class, namely—
 - (a) Ordinary Members: An Ordinary Member if financial shall have the following rights and privileges:—
 - (i) To be present and to speak and vote at Ordinary, Special or Annual General Meetings of The Society, to vote in postal ballots conducted by The Society, and to attend excursions, meetings, lectures or other activities arranged from time to time by The Society.
 - (ii) To be eligible for election as a member of the Council hereinafter referred to and also to any office or position in The Society.
 - (iii) To submit to the Council for consideration for publication papers prepared by any such member on any scientific subject.
 - (iv) To submit to the Council for consideration for publication on behalf of authors not resident in Western Australia, papers written by such authors on any scientific subject.
 - (v) To receive the Journal of The Society.
 - (vi) To receive other publications or documents issued by The Society, upon such conditions as the Council may from time to time determine.
 - (vii) To borrow books, periodicals, papers, or other documents belonging to The Society, subject to the approval of the Council.

- (viii) To propose or second candidates for admission as Ordinary, Associate or Student Members of The Society.
 - (ix) With the previous approval or assent of the Council or President, or duly appointed chairman or leader of any meeting held by The Society, to introduce visitors. Such visitors shall not be entitled to vote at any such meeting or excursion, but may express opinions on any matter under discussion at the invitation of the chairman or leader.
 - (x) To propose or second any Honorary or financial Ordinary Member for election to Council.
- (b) Associate Members: Persons elected as Associate Members shall be entitled to attend and speak at general meetings, excursions and other activities conducted by The Society, but shall not be entitled to vote at any meeting, and if any such member should vote, then that vote shall not be counted. Associate Members shall be entitled to submit papers for publication, to receive publications or documents issued by The Society at a price fixed by the Council from time to time and subject to the approval of the Council, may borrow books, periodicals or other documents belonging to The Society, but shall not be entitled to be proposed for, or elected to, any office in The Society, nor to propose or second others for membership or office in The Society.
- (c) Student Members: The Council may, on application to be made each year in such form it may require, admit as Student Members, persons under the age of twenty five years who are undertaking formal studies in Western Australia. Student Members shall have the same rights and privileges, and shall be subject to the same restrictions, as Associate Members.
- (d) Honorary Members: The Society at its Annual General Meeting in any year may, on the recommendation of the Council, admit as Honorary Members persons distinguished in Science or as patrons thereof, but only in so far as the number of such members shall not at any time exceed twenty five. Honorary Members shall have the same rights and privileges as Ordinary Members, but without liability for any subscription.
- (e) Honorary Associate Members: The Society at its Annual General Meeting in any year may, on the recommendation of the Council, admit as Honorary Associate Members persons interested in science, but only in so far as the number of such members shall not exceed twenty five. Honorary Associate Members shall have the same rights and privileges, and be subject to the same restrictions, as Associate Members, but without liability for any subscription.
- (f) Corporate Members: Corporate membership may be made available by the Council to organizations under such terms and with such rights and privileges as the Council may determine.
12. Every person desirous of becoming an Ordinary or Associate Member of The Society shall make application in the form prescribed from time to time by the Council and shall be proposed by an Ordinary or Honorary Member of The Society and seconded by at least two other Ordinary or Honorary Members of The Society, to each of whom the applicant is known personally. Each application shall be accompanied by the subscription applicable to the class of membership sought and shall be lodged with one of the Secretaries. Each Ordinary and Honorary Member of The Society shall be informed of the application forthwith by such means as the Council may from time to time determine. The Council shall accept or reject each candidate at a meeting of the Council held not less than one month and not more than six months after issue of advice of the candidate's application to the Ordinary and Honorary Members. Ordinary or Honorary Members wishing to object to admission of any candidate shall communicate their objection and the reasons for it to the President within one month of the issue of such advice. The President shall investigate any such objection and shall report the results of his investigation to the Council, but shall not reveal the identity of the Ordinary or Honorary Member lodging such objection. The Council shall consider the President's report, and shall determine by vote to admit or not admit the candidate to the class of membership sought. Admission shall be made by a two thirds majority of those Council members present and voting.
13. The Secretary shall inform each candidate of his admission or non-admission to the class of membership sought. Upon admission, each Ordinary or Associate Member shall receive a copy of The Society's Constitution and Rules and Regulations. His membership shall be deemed to apply to the whole of the financial year in which he was admitted so that, subject to their availability, he shall be entitled to receive all publications and documents issued during that year to all members of his class.
14. Every member of The Society, of whatever class, shall be bound to observe and perform, and not commit any breach of, the Rules and Regulations of The Society from time to time in force.
15. Every member shall notify the Secretary in writing of the address to which he may desire notices or communications to be forwarded to him, and shall from time to time notify in writing any change in such address. If any member shall fail to give such notification he shall have no claim against The Society for publications or notices of the meetings or other activities of The Society; no meetings or other proceedings shall be invalidated by reason of any such member not having received such notice.
16. Any member, on paying to The Society all subscriptions or moneys owed by him and returning all books, papers, manuscripts, or property of The Society which may have been borrowed or received by him, may resign his membership by giving notice in writing to the Secretary of The Society; and any member ceasing by resignation, death, or otherwise to be a member of The Society shall not, nor shall his representatives have any claim upon or

interest in the funds or property of The Society; but nothing herein contained shall prejudice the right of The Society to recover any moneys owing or property of The Society borrowed, held, or received by such member at any time.

17. Any member whose subscription may be in arrears for a period of at least two years shall, on a resolution of the Council being at any time thereafter passed, be declared to be no longer a member and thereupon shall cease to have the rights and privileges to which he may have been entitled; provided always that nothing herein contained shall prejudice the right of The Society to recover from such member all moneys or subscriptions due, owing, or payable by him up to the date of such termination of his membership, and also to recover all books, papers, manuscripts, or property belonging to The Society which may be held or have been received by such member at any time.
18. Every member in the respective classes of membership in The Society shall use his best efforts to promote the objects of The Society and shall not do or commit any act, deed, or thing which may be deemed by the Council to be prejudicial to the interests of The Society.
19. The Council may, by an affirmative vote of two thirds of its total membership, remove or suspend from membership or expel any member of The Society without being required to assign any reason for such action. Notice of such removal, suspension, or expulsion, shall be sent by registered post to the last known address of the member concerned within seven days after the decision of the Council. Any member against whom such decision of removal, suspension, or expulsion shall be made, shall be entitled to appeal to a Special General Meeting of The Society by notice to be forwarded by him in writing, addressed to the Secretary within two months after the date of such removal, suspension, or expulsion, stating in such notice the grounds of appeal. It shall be the duty of the Council to summon a Special General Meeting of The Society for the purpose of considering any such appeal, and of hearing statements by any Member of the Council or by the member who may have been removed, suspended, or expelled, and if a majority of the members present at such meeting uphold the decision of the Council, then the decision of the Council shall be confirmed, but if such majority shall uphold the appeal, then the decision to remove, suspend, or expel such member shall be set aside. No such member shall be entitled to exercise such right of appeal after the expiration of the said period of two months. In the event of any such removal, suspension, or expulsion taking effect, the member concerned shall remain liable for all moneys or subscriptions due or payable by him as at the date of such removal, suspension, or expulsion, and for the return of all property belonging to The Society.

Subscriptions

20. The subscription for each ordinary membership shall be set from time to time on recommendation of Council and approval by a resolution passed by a two-thirds majority of Ordinary Members voting at any Ordinary or Annual General Meeting of The Society, of which at

least twenty eight days notice has been given, and in which notice the proposed alterations have been specified.

An Ordinary Member, whose subscription is not in arrears, may at any time compound for the subscription for the current year and for all future years during the life of such member on payment of a fee of:

- (a) twenty years subscription at the rate of the current year or
 - (b) such sums as will, together with the annual subscriptions already paid, make a total equal to thirty years subscription at the rate for the current year.
21. Associate Membership shall not be more than 60% of the Ordinary Membership rate.
 22. Student Membership shall not be more than 20% of the Ordinary Membership rate.
 23. The financial year of The Society shall be from the first day of July in each year to the thirtieth day of June in the following year.
 24. All subscriptions shall be payable in advance and shall become due on the first day of July in each year. Any member whose subscription is unpaid three months after the due date in any year shall be deemed to be not financial.

Management

25. The management of the business and affairs of The Society shall be vested in a Council consisting of a President, two Vice-Presidents, Treasurer, two Secretaries, Librarian, Editor, Immediate Past President and eight Ordinary or Honorary Members of The Society.
26. All members of the Council shall be elected annually at the Annual General Meeting of The Society to be held on a date normally in July at a place to be decided by the Council. For the purpose of such election, the Council then in office shall submit at an Ordinary or Special General Meeting held not less than one calendar month before the Annual General Meeting, a list of names of Honorary or financial Ordinary Members proposed by the Council for election for the ensuing year and shall appoint a Returning Officer. Any Ordinary or Honorary Member present at such Ordinary General Meeting shall be entitled to propose another financial Ordinary or any Honorary Member to hold any position on the Council, and if such nomination be duly seconded and if the candidate nominated has signified his willingness to accept office if elected, then the name of such nominee shall be added as a candidate. Further, any Ordinary or Honorary Member of The Society may lodge with the Returning Officer within seven days after that Ordinary or Special General Meeting, preceding the Annual General Meeting, a nomination in writing in favour of any financial Ordinary or any Honorary Member for any position on the Council. Such written nomination shall be seconded by another Ordinary or Honorary Member, and shall carry a statement by the candidate nominated as to his willingness to accept the office if elected. Upon receipt of such nomination, the Returning Officer

- shall add the name of the nominee as a candidate for the Council.
27. If the number of members duly proposed for election does not exceed the number of vacancies for the various offices, the Chairman of the Annual General Meeting shall declare the persons nominated as duly elected. If the number of nominations for any office exceeds the number of vacancies, an election shall be held and the results ascertained by preferential ballot. For the purpose of such election, a ballot paper containing the names of all persons duly proposed for all contested positions on the Council shall be prepared by the Returning Officer and sent to all Ordinary and Honorary Members. Such members desirous of voting shall cause to be delivered to the Returning Officer such ballot papers, duly completed in accordance with any instructions on voting procedure before the formal opening of the Annual General Meeting. The Annual General Meeting shall appoint at least two scrutineers, who shall examine the procedures of the Returning Officer in his counting of votes and who shall report the results of his count to the Chairman of the Annual General Meeting. Such Chairman shall announce the result of the ballot at the Annual General Meeting or at the next Ordinary or Special General Meeting of The Society.
 28. All members of the Council shall be eligible for re-election, and each Council duly elected shall hold office until results of the next annual election are announced at an Annual or Ordinary or Special General Meeting or otherwise communicated to The Society.
 29. Any casual vacancy in the Council may be filled by resolution of the Council, and any member so appointed shall hold office until the next annual election of Council. Any vacancy not filled at the annual election shall be deemed a casual vacancy.
 30. The Council may define the duties of the two Secretaries and may add any distinguishing word to the title of one or both Secretaries in accordance with the nature of the duties to be performed.
 31. The Council shall meet at least once in each month from February to November inclusive in each year (unless otherwise decided by Council), at such times and places as may be appointed by the President, or in his absence, by one of the Vice-Presidents, and due and sufficient notice shall be previously sent to each member of the Council.
 32. A quorum for a meeting of the Council shall be the President or one of the Vice-Presidents, a Secretary who may be specially appointed for that meeting, and four other members of the Council, and no business shall be transacted at any Council meeting unless such quorum is present.
 33. If any member of the Council (including holders of offices) shall fail to attend three consecutive meetings of the Council without satisfactory explanation or reason, or without leave of absence having been first granted to him, then the position or office of such member may by resolution of the Council be declared vacant, and on passing of such resolution he shall cease to be a member of Council and holder of any office to which he may have been elected.
 34. The Council shall present at each Annual General Meeting a report giving a review of the work of The Society during the preceding year and some details and information with regard to its progress and affairs, and shall publish this report.
 35. The Council may appoint a Committee of such number as the Council may decide to consider and make recommendations on any subject on which the Council may require advice provided that such Committee include at least one Council Member. Each Committee so appointed shall be reviewed at regular intervals to be determined by the Council.
 36. The Council may from time to time make, alter, and repeal by-laws to enable it more effectually to carry out the management of the affairs of The Society, and to regulate the conduct of members and assist in the protection of its property, and for such purposes as may be calculated to advance the welfare of The Society, provided that such changes are not inconsistent with these Rules and Regulations.
 37. The Council, without limiting its general powers of management and carrying on the business and affairs of The Society, may exercise and do all things necessary except such as may be required or directed to be exercised by General Meetings, including power to appoint and remove all or any officers, assistants, employees, or others deemed by the Council to be necessary in connection with the work of The Society, and that with or without remuneration and upon such terms and conditions as the Council may think fit. The Council may also delegate all or any of its powers or authorities to any committee or sub-committee from time to time, and may pay all or any expenses or liabilities incurred from time to time and take any steps or proceedings which may be deemed desirable for the purpose of carrying out or securing the fulfilment of any of the objects or purposes of The Society.
- President and Vice-Presidents*
38. The duties of the President shall be to preside at all meetings of The Society and Council, and regulate all the proceedings therein and generally to execute or see to the execution of the Rules and Regulations and by-laws of The Society. In the case of an equality of votes at any meeting, the President or Vice-President or member presiding shall have a casting vote in addition to a deliberative vote.
 39. In the absence of the President from any meeting of the Council, his place shall be filled by one of the Vice-Presidents. In the absence of the President from any other meeting or excursion of The Society, his place shall be filled by one of the Vice-Presidents or by an Ordinary or Honorary Member of The Society elected as Chairman or leader by the Ordinary and Honorary Members there present.
- Duties of Officers*
40. The Secretaries shall conduct correspondence, cause notices of meetings to be sent out, keep adequate records of all meetings and other activities of The Society, and

generally perform such duties as are usually assigned to persons holding such office and comply with the directions, requests, or instructions issued from time to time by the Council.

41. The Treasurer shall keep a correct record of all receipts and disbursements, including subscriptions and all moneys received for the benefit of The Society, and shall pay those moneys forthwith to the credit of The Society at its bankers. It shall be the duty of the Treasurer to pay all accounts passed by the Council. No moneys shall be withdrawn from the bank account except by cheque signed by any two of a group of three which shall include the President, Treasurer and another member of The Society so authorized by the Council. The Treasurer shall cause the books of The Society to be posted regularly, and shall bring his books to balance as on the thirtieth day of June in each year, or on such other date as the Council may from time to time decide.
42. The Treasurer shall annually submit to an Auditor or Auditors all books and accounts kept by him in connection with the affairs of The Society, made up to the date last mentioned. The Society shall, not later than its Ordinary General Meeting immediately prior to the Annual General Meeting, appoint some person or persons to be Auditor or Auditors, but if such Ordinary General Meeting shall fail to make such appointment, then the Council may appoint an Auditor or Auditors.
43. It shall be the duty of the Auditor or Auditors of The Society to submit a written report each year on the financial affairs of The Society through the Council to an Ordinary, Special or Annual General Meeting of The Society.
44. The Librarian shall maintain records and generally manage the books, periodicals and documents of The Society according to the directions of the Council.
45. The Editor shall supervise the production and distribution of The Society's Journal and such other publications as the Council may direct.
46. Other members of the Council shall assist in the general management of The Society according to the needs which may arise from time to time.

Ordinary General Meetings

47. Ordinary General Meetings of The Society shall be held at 8 p.m. on the third Monday of the months March to June and August to December inclusive in each year, unless the Council determines otherwise, but at least three Ordinary General Meetings shall be held in each financial year. Notice of each Ordinary General Meeting shall be sent to all members of each class. A quorum for an Ordinary General Meeting shall be seven Ordinary or Honorary Members personally present. Conduct of an Ordinary General Meeting shall be at the discretion of the President or Chairman elected by such meeting.

Annual General Meetings

48. The Annual General Meeting of The Society shall, unless the Council determines otherwise, be held on the third Monday of July in each year at a time and place

determined by the Council. Notice of each Annual General Meeting shall be sent to all members of each class at least one calendar month before such meeting.

49. The proceedings of the Annual General Meeting, unless otherwise determined by the Council, shall be as follows:—
 - (a) Presentation of the minutes of the previous Annual General Meeting.
 - (b) Reading of nominations of candidates for Council, appointment of scrutineers, and counting of votes.
 - (c) Presentation of the Annual Report of the Council.
 - (d) Presentation of the Balance Sheet, Statement of Accounts and (if available) Auditor's Report.
 - (e) Report (if available) of the scrutineers on the ballot and declaration of the results by the retiring President.
 - (f) Address by the retiring President.
 - (g) Installation of the new President.
 - (h) Any other business of which notice may have been given or agreed by the meeting to be considered.
50. A quorum for transaction of business at an Annual General Meeting shall be seven Ordinary or Honorary Members of The Society personally present.

Special General Meetings

51. Special General Meetings of The Society may be called by the Council whenever it may deem such meeting expedient, or on the requisition of ten Ordinary or Honorary Members made in writing to one of the Secretaries and specifying the purpose for which the meeting is required. Upon receipt of such requisition, that Secretary shall call the meeting within not less than seven days nor more than twenty eight days. Notice of such meeting shall be sent to all members of each class. The Chairman of the meeting shall be the President or a Vice-President or, in their absence, an Ordinary or Honorary Member elected by the meeting.
52. A quorum for a Special General Meeting of The Society shall be seven Ordinary or Honorary Members personally present.

The Journal of the Society

53. The Society shall publish a Journal at least once a year, in which papers communicated to The Society during or before that year may be printed. The Journal shall be printed in such form as may be decided by the Council.
54. Every paper intended to be published in the Society's Journal must be sent to the Editor for consideration by a Publications Committee appointed by the Council. The Editor shall be Chairman of the Publications Committee.
55. The Publications Committee shall obtain an expert opinion from any person or persons it may select as referees to judge the suitability of any paper for publication. The Committee shall communicate to the Council the Com-

mittee's recommendation on whether or not a paper submitted for publication should be accepted for the Society's Journal.

56. It shall be the duty of the Council to decide, on the recommendation of the Publications Committee, whether or not a contribution shall be accepted for publication.
57. All papers accepted for publication must be read or otherwise communicated at an Ordinary, Annual or Special General Meeting prior to publication. The Council shall decide if a paper shall be read in full, in abstract, or taken as read.
58. Publication in the Society's Journal shall be available to all categories of members and to non-members resident outside Western Australia. Papers by non-members resident outside Western Australia shall be communicated through an Ordinary or Honorary Member.
59. The original copy of every paper accepted for publication by The Society, with its illustrations, shall become the property of The Society, unless the Council decides otherwise. Authors shall not be at liberty to publish elsewhere papers submitted to The Society for publication in its Journal, unless permission for doing so is given by the Council, or unless the Society fails to publish the paper in the Journal of the year in which it is accepted or of the succeeding year, or does not accept the paper for publication.
60. The published price of the Journal shall be fixed by the Council from time to time.
61. Offprints of papers shall be available to authors on such terms as shall be decided from time to time by the Council.

The Medal of the Royal Society of Western Australia

62. A medal shall be awarded by the Council every fourth year or at such other times or periods as the Council may from time to time decide for distinguished work in science connected with Western Australia. The Council shall appoint a Medal Committee consisting of five members of the Council to recommend a recipient of the medal.

Formation of Sections

63. Sections may be formed for the purpose of any particular branch of science. Any member of The Society may be enrolled as a member of one or more sections. Each

section shall appoint a Chairman and Secretary, who shall be approved by the Council. Sections shall not incur expenditure without first obtaining the approval of the Council. Any communication to a section may be presented subsequently at a general meeting of The Society.

Common Seal

64. The Common Seal of The Society shall be in the custody of the President or one of the Vice-Presidents, and the President or any one Vice-President shall respectively be authorized to use the same, and when required to be affixed to any deed, document, or writing, shall be so affixed by either the President or one of the Vice-Presidents and signed by him and countersigned by a Secretary of The Society.

Interpretation of the Constitution and Rules and Regulations

65. The Council of The Society shall be the sole authority for the interpretation of the Constitution and of the Rules and Regulations of The Society, and the decisions of the Council on questions of interpretation shall be final and binding on all members.
66. The Constitution or the Rules and Regulations or any of them may be amended, altered, enlarged or repealed from time to time by a resolution passed by a two thirds majority of Ordinary or Honorary Members voting in a postal ballot conducted by the Council. Notice of intention to conduct such a ballot shall be given with notice of an impending Ordinary or Annual or Special General Meeting of The Society and the proposed amendment or amendments shall be presented at that meeting at least one calendar month before the ballot is held.

Winding up of The Society

67. The Society may be wound up by a resolution to be passed by a four fifths majority of the Ordinary Members of The Society present and voting at a Special General Meeting summoned for such purpose, whereof at least twenty eight days notice shall be given. If a resolution to wind up be passed, all property and assets of The Society shall be disposed of or applied in such manner as may be decided at such meeting.

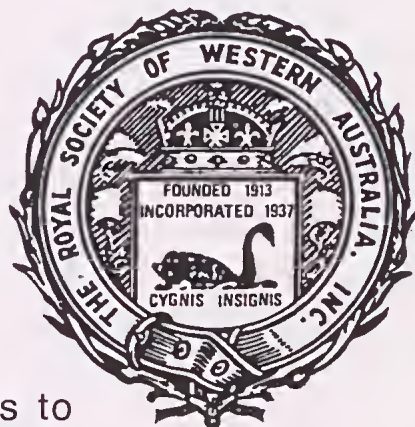
Why you should join The Royal Society of Western Australia

Relevance

- The Royal Society of Western Australia - the State's main cross-disciplinary scientific body - exists to promote and assist in the advancement of science in Western Australia.

The Society provides an avenue for scientists to demonstrate the value of their work to the community, and helps to educate the lay person and fellow scientists.

The Royal Society of Western Australia was modelled on the world's oldest and best known scientific society, The Royal Society of London. Both groups are important in overcoming the narrowing effects of specialization.



Publications

- The Society's publications are in high demand. The high quality and reputable Journal has been published for 80 years, and reaches more than 40 countries. Special issues from Symposia command special attention.

Symposia and Excursions

- Symposia and excursions held by the Society are of immense value to scientists and the community. Examples are the highly successful Leeuwin Current Symposium and a recent geological excursion to Rottnest Island.

Talks

- The Society promotes science at its montly meetings. Topics of talks are as broad as the interests of the members - from preservation of material from shipwrecks to Chaos Theory. Politicians from major parties recently gave their views on the role of science in society.

Join Today

- Join the Royal Society of Western Australia today and help give science a voice in Western Australia. No special academic qualifications are required.



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Interpretation of the Constitution and Rules and Regulations

65. The Council of The Society shall be the sole authority for the interpretation of the Constitution and of the Rules and Regulations of The Society, and the decisions of the Council on questions of interpretation shall be final and binding on all members.
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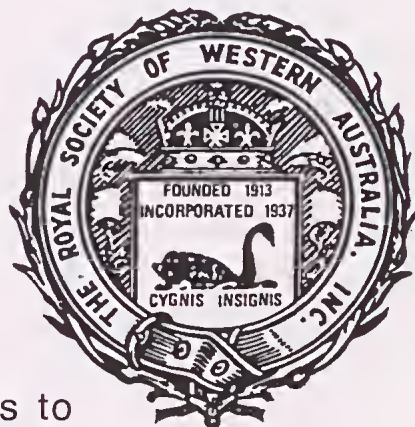
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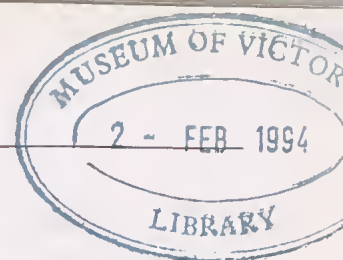
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Recent Advances in Science in Western Australia

Earth Sciences

A multi-authored collection of papers, edited by S K Skwarko of the Geological Survey of Western Australia, reviews all fossils described from the Permian of Western Australia, nearly one thousand species belonging to 22 fossil groups. An introductory chapter briefly surveys Permian palaeogeography, palaeoclimate and stratigraphic correlation.

Skwarko S K 1993 Palaeontology of the Permian of Western Australia. Geological Survey of Western Australia Bulletin 136.

The Tumblagooda Sandstone, deposited dominantly by fluvial processes on a palaeoslope to the northwest, is described by N H Trewin, of the University of Aberdeen, as interbedded fluvial and aeolian sandstone and dune deposits in which winds blowing obliquely up the palaeoslope to the southeast reworked the sandy, unvegetated and unconsolidated surface. Similar mixed fluvial and aeolian environments are considered to have been frequent in a wide range of climatic regimes prior to the abundance of land plants.

Trewin N H 1993 Controls on fluvial deposition in mixed fluvial and aeolian facies within the Tumblagooda Sandstone (Late Silurian of Western Australia). *Sedimentary Geology* 85:387-400.

The several interacting factors described by K H Morgan that have shaped the palaeodrainage systems of the Yilgarn Craton include land form prior to the breakup of Gondwana, breakup from Cretaceous to early Cainozoic, northward migration of the craton, and a number of distinct climatic cycles. The existing palaeochannels that were incised during the Early Eocene contain sedimentary sequences related to depositional and erosional cycles from the Late Eocene to the present. Valuable mineral deposits resulting from hydrochemical reaction with sediments include gold, uranium, alunite and gypsum. The palaeochannels contain water resources and potentially valuable lignite and limestone.

Morgan K H 1993 Development, sedimentation and economic potential of palaeoriver systems of the Yilgarn Craton of Western Australia. *Sedimentary Geology* 85:637-656.

The abundance of the normally tropical foraminiferan *Marginopora vertebralis* in southern Australian waters is attributed by J H Cann, of the University of Western Australia, and J D A Clarke, of Western Mining Corporation, to the warm Leeuwin current. They suggest that the presence of *M. vertebralis* in Last Interglacial sediments in the Glanville Formation in northern Spencer Gulf indicates a greater ecological influence of the palaeo-Leeuwin current across the continental shelf of southern Australia during periods of global warming and correspondingly higher sea levels.

Cann J H & Clarke J D A 1993 The significance of *Marginopora vertebralis* (Foraminifera) in surficial sediments at Esperance, Western Australia, and in Last Interglacial sediments in northern Spencer Gulf, South Australia. *Marine Geology* 111:171-187.

J S Myers, of the Geological Survey of Western Australia, describes the West Australian Craton and its adjacent orogens that have a Precambrian history of repeated generation, dispersal and aggregation of continental crust. Major episodes of collision and aggregation that occurred at 2700-2600, 2000-1800, 1300-1100 and 700-600 Ma coincide with similar activity in other Precambrian crust, and may reflect the formation of Precambrian supercontinents.

Myers J S 1993 Precambrian history of the West Australian Craton and adjacent orogens. *Annual Review of Earth and Planetary Sciences* 21:453-485.

Life Sciences

A cladistic analysis by A G Kluge, of the University of Michigan, presents a monophyletic classification of pythonine snakes based on an evaluation of all of the available evidence, mainly anatomical. The analysis concludes that the earliest pythonine radiations occurred in the Australian region.

Kluge A G 1993 *Aspidites* and the phylogeny of pythonine snakes. Records of the Australian Museum, Supplement 19.

Measurement of diurnal and seasonal water relations by J Dodd (WA Department of Agriculture) and D T Bell (University of Western Australia) of *Banksia* woodland canopy and understorey species indicate variable responses to summer drought. Water use was greater for canopy species (61% of total). Most canopy and understorey species depend on soil-stored water, and use most water in early summer (understorey) or late summer (canopy).

Dodd J & Bell D T 1993 Water relations of the canopy species in a *Banksia* woodland, Swan Coastal Plain, Western Australia. *Australian Journal of Ecology* 18: 281-293.

Dodd J & Bell D T 1993 Water relations of understorey shrubs in a *Banksia* woodland, Swan Coastal Plain, Western Australia. *Australian Journal of Ecology* 18:295-305.

Using protein electrophoresis, L Christidis of the Victorian Museum and R Schodde of the CSIRO Division of Wildlife Ecology (Lyneham) distinguish three primary lineages of meliphagine honeyeaters, *Lichenostomus*, *Meliphaga* and *Xanthotis*. The evolutionary radiations of honeyeaters are related to Plio-Pleistocene environmental oscillations in Australia and New Guinea.

Christidis L & Schodde R 1993 Relationships and radiations in the meliphagine honeyeaters, *Meliphaga*, *Lichenostomus* and *Xanthotis* (Aves: Meliphagidae): protein evidence and its integration with morphology and ecogeography. *Australian Journal of Zoology* 41:292-316.

Reproductive studies of females of the critically-endangered western swamp tortoise, by G Kuchling and S D Bradshaw of the University of Western Australia, indicate that vitellogenesis begins during summer aestivation and continues during autumn and winter, similar to many other chelids, but the timing of ovulation, which occurs in late September after a feeding bout that greatly increases body mass, is different.

Kuchling G & Bradshaw S D 1993 Ovarian cycle and egg production of the western swamp tortoise *Pseudemydura umbrina* (Testudines: Chelidae) in the wild and in captivity. *Journal of Zoology, London* 229:405-419.

A comprehensive ecological survey of the Abydos-Woodstock Reserve by various members of the Western Australian Museum summarises the history and land-use, physiography and climate, geology and soils, vegetation and habitats, and the invertebrate and vertebrate fauna, and makes management recommendations.

Western Australian Museum 1991 Ecological survey of Abydos-Woodstock Reserve, Western Australia. Records of the Western Australian Museum, Supplement 37.

J B Hutchins and K N Smith, of the Western Australian Museum, present a comprehensive catalogue of the type specimens of fishes in the collection of the Western Australian Museum.

Hutchins J B & Smith K N 1991 A catalogue of type specimens of fishes in the Western Australian Museum. Records of the Western Australian Museum, Supplement 38.

Physical Sciences

Gas chromatographic-mass spectrophotometric analysis of weathered bitumens from coastal Western Australian locations by researchers at Curtin University of Technology indicate biomarkers such as bicadinanes, which are believed to be derived from a tropical angiosperm, and suggest that these bitumens may have been transported from South East Asia to Western Australia by the Leeuwin Current.

Currie T J, Alexander R & Kagi R I 1992 Coastal bitumens from Western Australia — long distance transport by ocean currents. *Organic Geochemistry* 18:595-601.

Polarised neutron diffraction (pnd) measurements made on the compound $[\text{Co}(\text{NH}_3)_5(\text{OH})_2][\text{Cr}(\text{CN})_6]$ by B N Figgis and E S Kucharski (University of Western Australia) and M Vrtis (Institut Laue-Langevin, France) surprisingly show that about one-third of the unpaired electrons arising from the chromium (III) anion are located on the cobalt atom and the amine protons of the cation.

Figgis B N, Kucharski E S & Vrtis M 1993 Spin and charge transfer through hydrogen bonding in $[\text{Co}(\text{NH}_3)_5(\text{OH})_2][\text{Cr}(\text{CN})_6]$. *Journal of the American Chemical Society* 115:176-181.

A model of the electric current distributions in electrochemical cells with parallel rectangular plates by researchers from the University of Western Australia, that does not make the usual assumption of one-dimensional flow, provides a more realistic estimation of the effects of electrode resistance and geometry in batteries.

Marshall S L & Wolff S K 1993 Calculation of ohmic resistance effects in rectangular electrodes of finite thickness. *Journal of Applied Electrochemistry* 23:443-451.

The measurement of the binding constants of alkali metal cations and the crown ether 18C6 by G Hefter of Murdoch University and M Salomon of the U. S. Army Power Sources Laboratory, in the solvent 2-cyanopyrimidine using conductance data, shows that the formation of these complexes and their electrical mobilities depend on the solvation of the complexed and uncomplexed cations. The observed behaviour has been related to that in other solvents of interest in high energy batteries.

Salomon M & Hefter G 1993 Mobilities of cation-macrocyclic ligand complexes. *Pure & Applied Chemistry* 65:1533-1540.

Calculation by I Bray (Flinders University) and A Stebovics (Murdoch university) of the total ionization cross-section and spin asymmetry for the electron-impact excitation of atomic hydrogen quantitatively agrees with experimental data, using previously developed convergent close-coupling formalism.

Bray I & Stebovics A T 1993 Calculation of the total ionization cross section and spin asymmetry in electron-hydrogen scattering from threshold to 500 eV. *Physical Review Letters* 70:746-749.

Note from the Hon Editor: This column helps to link the various disciplines and inform others of the broad spectrum of achievements of WA scientists (or others writing about WA).

Contributions to "Recent Advances in Science in Western Australia" are welcome, and may include papers that have caught your attention or that you believe may interest other scientists in Western Australia and abroad. Papers in refereed journals, or books, chapters and reviews will be accepted. Abstracts from conference proceedings will not be accepted. Please submit short (2-3 sentences) summaries of recent papers, together with a copy of the title, abstract and authors' names and addresses, to the Honorary Editor (c/o Western Australian Museum) or a member of the Publications Committee: Dr S D Hopper (Life Sciences), Dr A E Cockbain (Earth Sciences), and Assoc. Prof. G Hefter (Physical Sciences). Final choice of articles is at the discretion of the Hon Editor.

"Letters to the Editor" concerning scientific issues of relevance to this journal are also published at the discretion of the Hon Editor. Please submit a word processing disk with letters, and suggest potential reviewers or respondents to your letter. *P C Withers, Hon Editor, Journal of the Royal Society of WA*

The mangrove systems of Western Australia: 1993 Presidential Address

V Semeniuk

21 Glenmere Road, Warwick, WA 6024

Manuscript received October 1993

Abstract

Mangroves of tropical Western Australia occur in subcontinental- to regional-scale sectors that are related to hinterland geomorphology, coastal processes and sedimentary provinces. The four main features that determine location and nature of the sectors are the style and amount of fluvial input from the hinterland to the coastal zone, the mineralogical nature of mud in the mangrove environment, the climatic setting of the coast, and the nature of the oceanographic regime that receives the sediment. From north to south the sectors are: Cambridge Gulf, with mangrove habitats in a tide-dominated estuarine-gulf environment; Kimberley Coast, with mangrove habitats in a tide-dominated ria-archipelago setting; King Sound, with mangrove habitats in a tide-dominated estuarine-gulf environment; Canning Coast, with mangrove habitats in barred to open tidal embayment settings; Pilbara Coast, with mangrove habitats in wave-dominated settings of deltas, barrier islands and ria-archipelago systems; Rowley Shelf Province, with mangrove habitats in small embayments and lagoons along the island shores and interior to islands; and Carnarvon Province, of uplifted limestone, with mangrove habitats in small embayments, deltas, and inland playas.

Within these coastal sector settings, there is a profusion of smaller scale habitats, the scale at which mangrove populations respond; these may be restricted to, and be distinctive of a particular setting. Combining the sectors with climate provides the best delineation of mangrove regions in Western Australia. This approach thus links climate [which determines species richness in a given area] with geomorphic-sedimentary setting [which determines whether habitats for particular species will be developed]. Accordingly, nine major mangrove regions are delineated on the availability of appropriate habitats and species richness in tropical Western Australia: Cambridge Gulf—semi-arid zone; Kimberley Coast—subhumid to humid zone; Kimberley Coast—semi-arid zone; King Sound—semi-arid zone; Canning Coast—semi-arid zone; Pilbara Coast—arid zone; Rowley Shelf Province—arid zone; and Carnarvon Province—arid zone.

Introduction

The diverse mangrove formations of northern tropical Western Australia inhabit a range of shore types between Shark Bay and Cambridge Gulf, and appear as a mosaic of complex systems along the coast. However, there are underlying physical patterns of geology, geomorphology, climate, coastal processes, and hydrology along this coast which help explain this complexity. My own interests in mangroves in these regions have been manifold, and the approach I have used in researching these systems has tended to be holistic and hierarchical, combining information on geology, geomorphology, sedimentology, soils, groundwater hydrology, and hinterland/shore interactions (e.g., Semeniuk 1983, 1985), with ecological and biological information such as mangrove species composition, structure, physiognomy and population maintenance (e.g., Semeniuk & Wurm 1987).

My research on the mangroves of Western Australia over the past 22 years has had four objectives. Firstly, to unravel the evolution of the coast from regional scale to small scale in

order to understand the development of mangrove habitats in tropical Western Australia. Secondly, to relate mangrove assemblages, populations and their zonation to habitats and gradients within habitats. Thirdly, to understand some of the mechanisms that maintain mangrove populations and that control their structure and physiognomy. Fourthly, to understand the various mechanisms that determine the survivorship and physiognomy of individual mangrove trees.

The first stage in this research was to establish a framework of coastal types so that the variety of types of smaller scale units that mangroves inhabit could be determined and studied in their spatial context, and any recurring pattern of habitats could be viewed in regional to subcontinental perspective. This paper concentrates on the results of research at that larger scale, to show the subcontinental scale patterns in the mangrove systems, to determine the reason for these patterns, and to describe some of the typical suites of habitats that are generated within the larger scale coastal types. A more detailed treatment of the mangrove systems at the smaller scales, e.g., within the habitats, in terms of stratigraphy, sedimentology, hydrology, mangrove population structures and floristics, is currently in preparation (Semeniuk in prep).

Information obtained at the subcontinental scale on coastal types and their suite of smaller-scale habitats for mangrove systems can be important in a number of ways—1. to understand the distribution of the different types of mangrove formations in this State, 2. as a framework for comparisons between the different mangrove systems along the coast, 3. to select coastal reserves, 4. for coastal managers to understand the types of coast and the structures and processes that make them host to mangroves, 5. to predict the effects of a potential sea level rise in response to global warming, and 6. as a framework for designating more detailed areas for further research. This approach also provides a basis for understanding species distribution and maintenance at the local scale. Also, since mangroves can be related to specific habitats, an inventory of habitats within a region can provide a valuable first indication as to what species can be expected, and where to find them, in a given area.

Material and Methods

Data in this paper are based mainly on fieldwork (e.g., Semeniuk 1980a,b, 1981a,b, 1982, 1983, 1985, 1986a, in prep; Semeniuk & Wurm 1987). Coasts not surveyed directly on the ground were examined and photographed by aerial survey, then studied using aerial photographs. In the field, mangrove systems were studied along transects where trenches, cores or augers were used to determine soil sequence and stratigraphy (Semeniuk & Wurm 1987). Samples from fieldwork were processed in the following manner (Semeniuk 1983, Semeniuk & Wurm 1987): binocular microscope examination; sieving (granulometry); thin section analysis of selected samples; acid digestion to determine carbonate content within the mud fraction; x-ray diffraction of selected mud fractions for more detailed mineralogic analysis; descriptions of cores; analysis of selected shells for ^{14}C ; and analysis of soilwater and groundwater for salinity. Terminology for geomorphic units, habitats and scale follows Semeniuk (1986a).

Overview of the Mangroves of Western Australia

Mangrove formations occupy extensive coastal tracts of the tropical northwestern part of Australia (Fig 1A). With a few notable exceptions, such as the cliffed rocky coasts along the tectonically uplifted Cape Range and Cape Cuvier peninsulas, and high-energy coastlines such as Eighty Mile Beach (Fig 1E), the mangroves form a nearly continuous fringe along the coast of Western Australia when viewed at the sub-continental scale. They span a climatic gradient from arid in the south to humid in the north (Bureau of Meteorology 1973, 1975; Gentili 1971, 1972; Fig 1B) and occur in a wide range of settings and habitats (Semeniuk, 1983, 1985, 1986b). The mangroves occur in tidal regimes from microtidal in the south to macrotidal in the north (Easton 1970; Davies 1977; Fig 1C), inhabiting the interval between mean sea level (MSL) and about mean high water spring tide (MHWS) in arid to semi-arid environments, and extending almost up to the position of equinoctial high water mark (EHWS) or highest astronomical tide (HAT) in more humid climates.

Mangroves inhabit coasts located in quite variable geological and geomorphic settings (Fig 1D), and hence occupy ria shores, tidal embayments, limestone barrier coasts, wave-dominated deltas, tide-dominated deltas, and beach/

dune shores, amongst others. These variable geological settings influence the relationship of hinterland to the tidal zone, and variation in this relationship, within diverse climate settings, results in differing types of hydrologic exchanges between freshwater and tidal zone hydrology. For instance, the hinterland / tidal interactions in the Kimberley area (ria coasts) contrasts with the deltaic and barrier island setting of the Pilbara region (Semeniuk 1983, 1985).

The mangroves of Western Australia occur along coasts that are also variable both in their modern dynamics (erosion vs accretion; wave-dominated conditions vs tide-dominated conditions; storm activity) and their Holocene sea level history. Many of these features are fundamental to the development of the different mangrove systems. For instance, the coast between Shark Bay and Port Hedland is wave-dominated, with wave climate due to swell and wind waves. As a result, many of the coastal landforms have been sculptured by wave and wind processes; some parts of this coast are delta-lands, others are barrier islands, others are beach / dune systems. In contrast, the Kimberley coast is tide-dominated and is of a markedly different character in terms of coastal style, with sedimentation and development of the main mangrove habitats confined to embayments.

To show the floristic, ecological and edaphic variability, a brief description of the mangrove systems of Western Australia is presented below in terms of 1. mangrove biogeography, zonation, structure, and physiognomy as related to climatic setting, 2. regional factors important in developing mangrove habitats, and 3. types of mangrove habitats.

Biogeography, zonation, structure, and physiognomy

There are 17 mangrove species in Western Australia (Semeniuk *et al.* 1978; Semeniuk 1983); these are: *Acanthus ebracteatus* Vahl, *Aegialitis annulata* R. Br., *Aegiceras corniculatum* (L.) Blanco, *Avicennia eucalyptifolia* Zipp. ex Miq., *Avicennia marina* (Forsk.) Vierh., *Bruguiera exaristata* Ding Hou, *Bruguiera parviflora* (Roxb.) Wight & Arn. ex Griff., *Camptostemon schultzei* Mast., *Ceriops tagal* (Perr.) C.B. Rob., *Excoecaria agallocha* L., *Lumnitzera racemosa* Willd., *Osbornia octodonta* F. Muell., *Pemphis acidula* J.R. & G. Forst., *Rhizophora stylosa* Griff., *Scyphiphora hydrophyllacea* Gaertn., *Sonneratia alba* Sm., *Xylocarpus australasicus* Ridley (may be = *X. mekongensis* Pierre; see discussion in Tomlinson 1986). The most common and widespread species are *A. marina*, *R. stylosa*, *B. exaristata*, *C. tagal*, *A. annulata* and *A. corniculatum*.

The distribution of mangrove species in Western Australia has been recorded by Saenger *et al.* (1977), Semeniuk *et al.* (1978), Wells (1981, 1982), Semeniuk (1983, 1985), and Bridgewater (1985). Fifteen species occur in the northern, humid parts of the region and this number progressively decreases towards the southern, more arid areas down to four species in Exmouth Gulf, and only one species in Shark Bay (Fig 1F).

Mangrove formations exhibit compositional zonation across the tidal zones (*cf* MacNae 1968). This zonation depends on the type of habitat (e.g., sandy tidal flat, muddy tidal flat, spit), type of physico-chemical gradient within the habitat (e.g., inundation frequency, salinity, grain size of substrate), and species pool. Variation of zonation of mangroves across the climatic regions of Western Australia

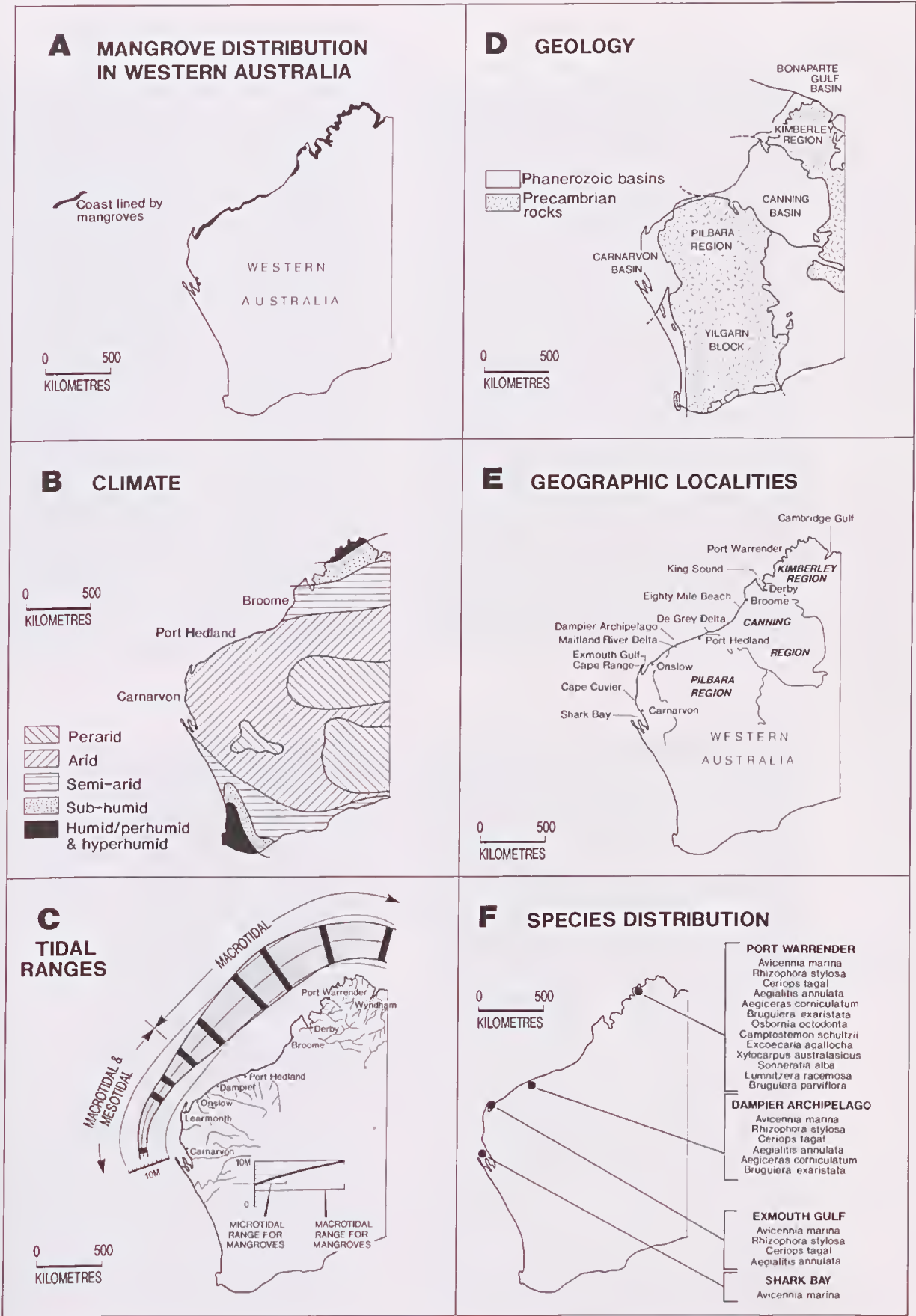


Figure 1. The subcontinental setting of mangroves in Western Australia: 1A: Distribution of mangroves in Western Australia. 1B: Climate setting (after Gentilli 1972). 1C: Tidal regime (data from Calder 1979). 1D: Geological setting (after Geological Survey of W.A. 1975), showing the variable geological provinces that the coast intersects. 1E: Main geographic locations mentioned in text. 1F: Change of species richness from humid northern areas to southern arid areas (data from Semeniuk *et al.* 1978)

and between habitat types across the different climatic regions of northern and northwestern Australia has been documented by Semenjuk *et al.* (1978) and Semenjuk (1983, 1985). In the species-rich tropical humid areas there is marked zonation of mangroves. For instance, on muddy tidal flats, there may be a seaward zone of *S. alba*, followed by a zone of *A. marina*, a zone of *C. schultzei* and then by *R. stylosa*, and finally a mixed landward zone of *A. marina*, *A. australis*, *B. exaristata* and locally pure stands of *C. tagal*. In arid zones, muddy tidal flats present a more simple sequence: a seaward zone of *A. marina*, a middle zone of *R. stylosa*, and a landward zone of *A. marina*, with local pure stands of *C. tagal*.

The mangrove formations in Western Australia also are variable in their structure and physiognomy in relationship to climate and to their position on the tidal flat. Tall forest formations tend to be common in the humid regions, and scrub and heath (also termed "dwarf forests" by some authors) in the more arid regions. Physiognomically, the mangrove trees and shrubs vary from being predominantly more slender-trunked in humid forest settings to recumbent, gnarled, or mallee-form in more arid settings. The structural and physiognomic variation within the mangroves across the tidal flat follows the gradients of decreasing frequency of inundation of seawater and increasing salinity of groundwater: forests, low forests and scrub dominate seaward parts of the mangrove formations, whereas scrub and heath dominate landward parts. Thus in humid areas there is gradation from forests in seaward parts of the mangrove formations to scrub and heath in landward parts, and in arid zones from recumbent and gnarled low forests and scrub in seaward parts to mallee-form heath and "dwarf forests" in landward parts of the formations. Where there is only one species of mangrove on the tidal flat (e.g., *Avicennia marina*), there often is a physiognomic and structural zonation in the mangrove belt in response to the physio-chemical gradients.

Regional factors important for developing mangrove habitats

Regional factors that determine the style of mangrove habitats developed in a given area are coastal setting, climate, and tidal range (Table 1). These factors are of course inter-related.

Table 1

Regional factors important in the development of mangrove systems

Coastal Setting

Sediment types
Stratigraphy

Climate

Rainfall & freshwater input
Evaporation
Cyclonic activity
Temperature
Wind

Tidal Range

Habitat availability
Coastal processes

Coastal setting, i.e., coastal geomorphology and geology, Quaternary geological history, the relationship of the coast to the differing types of hinterland, and the oceanographic setting, determine the basin setting for mangrove habitation, the coastal processes extant at a given site, and the types of sediments and stratigraphy that will underlie mangrove systems. These features are important in developing the edaphic setting of the mangrove habitats.

The important aspects of climate are: rainfall which determines the freshwater input into the tidal system either directly or via groundwater discharges (Semenjuk 1983); evaporation which places physiological stress on mangroves, and develops high salinity on the tidal flats; cyclonic activity which affects mangroves themselves, as well as modifies coasts and habitats; and temperature. Wind is important because it generates waves, and develops spits (as local habitats for mangroves; Figs 2A, B) and builds coastal dunes. These dunes can be important in mangrove systems: at larger scales they can develop lagoon/dune complexes and also form the ridge and swale systems of wave-dominated deltas; at smaller scales they function as reservoirs of freshwater—as a result the hydrologic interface between dunes and their junction with the tidal zone often becomes a local mangrove habitat; and mobile dunes can locally encroach upon and kill mangroves (Fig 2C).

Tidal range influences the development of mangrove habitats in two ways. Firstly, the size of the tidal range determines the amount of tidal flat exposed for mangrove habitation. Secondly, the tidal range determines whether the coast will develop tide-dominated (or at least tide-influenced) coastal landforms.

As a result of all of these factors, there are developed a number of coastal systems at the regional scale that are host to mangroves in Western Australia. These include: wave-dominated deltas, tide-dominated deltas, barrier islands, tidal creek systems, embayments, ria shore and archipelago systems, dune coasts, lagoon systems, and island complexes. The occurrence of these coastal types within sectors in Western Australia are described below.

Mangrove habitats and assemblages

Within the regional-scale coastal types listed above, there is a profusion of habitat types for mangroves, many of which are restricted to a given coastal setting. Thus, for instance, in ria shore settings regardless of whether they are located in the Kimberley region or in the Pilbara, there are tidal flats, high tidal alluvial fans, rocky shores and tidal creeks. In wave-dominated deltaic settings there are lagoons in the inter-ridge swales, muddy tidal flats, sandy tidal flats and tidal creeks. Within many of the regional-scale coastal types there also may be recurring patterns of habitat types: for instance, spits, cheniers, and sandy beaches are coastal features that occur in a wide variety of regional-scale coastal settings.

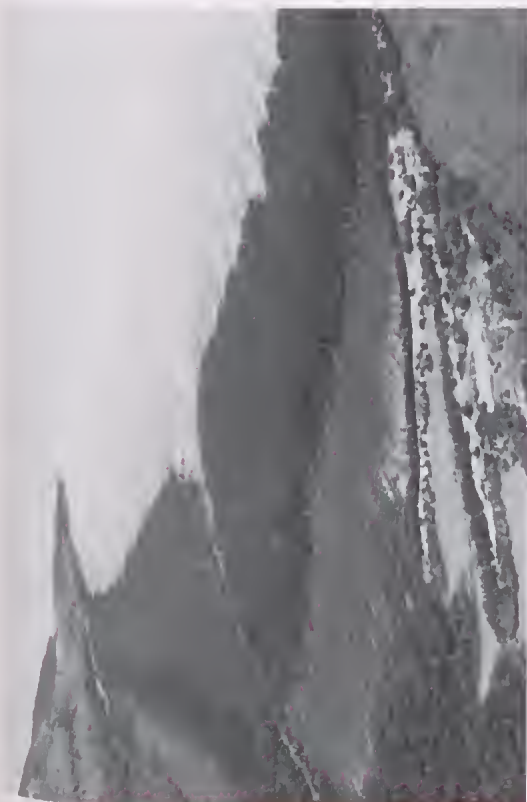
The combination of geomorphology, substrates, stratigraphy, aquifers and salinity at small scales within the regional-scale coastal types develops the various habitats for the mangroves. The main mangrove habitats in Western Australia are: muddy tidal flats, sandy tidal flats, gravelly



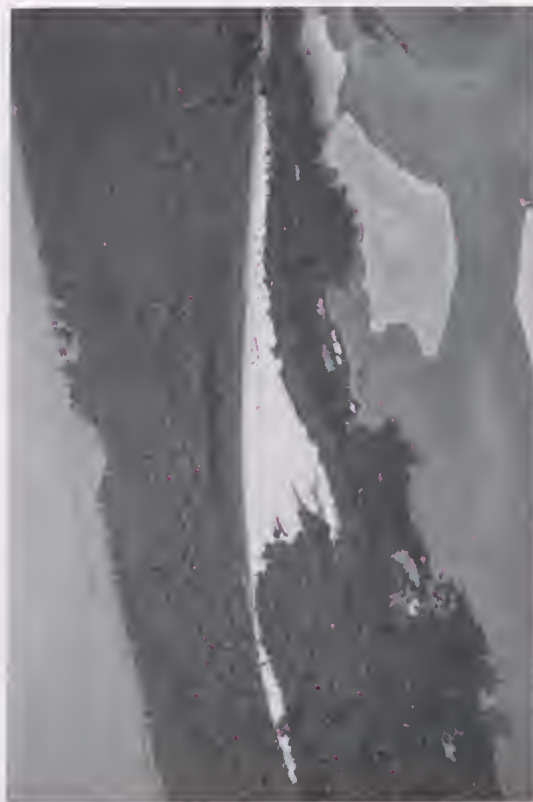
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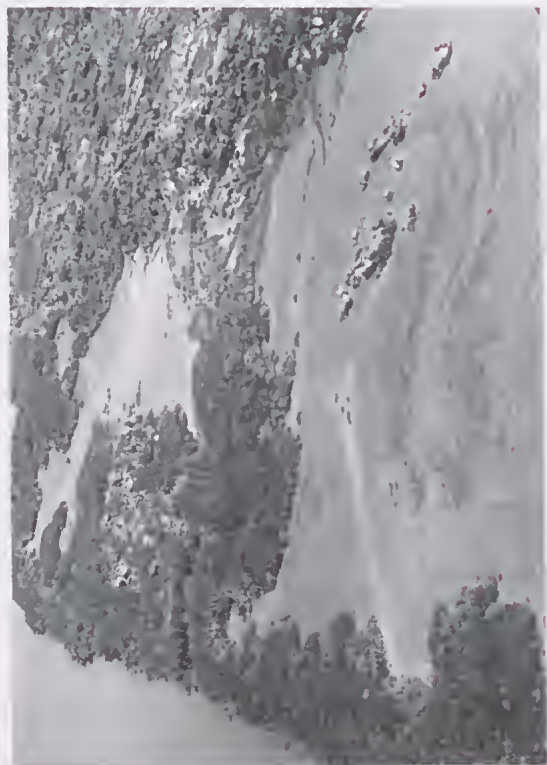
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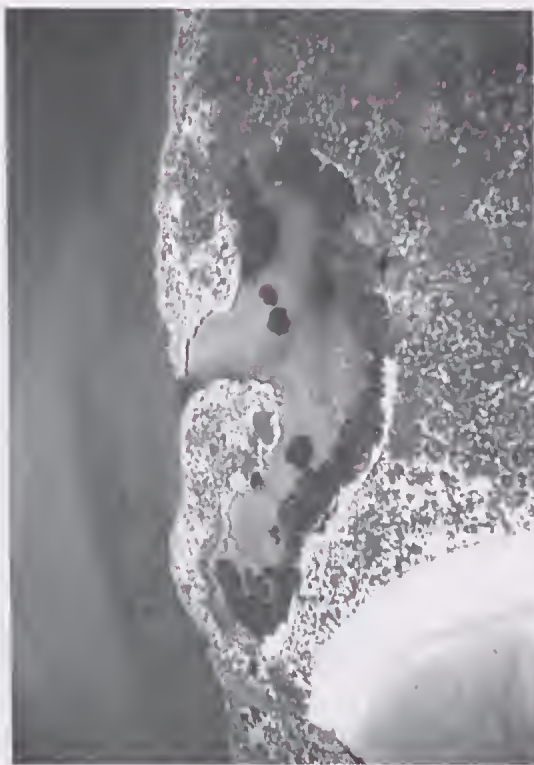
(2B)

Figure 2. Various small-scale habitats for mangroves, drawn from wide ranging locations, from the Kimberley Coast to the Pilbara to illustrate the wide variety and styles of mangrove habitats. **2A:** Spits, fringed by mangroves, emanating from a headland in a ria setting, Port Warrender area; also visible are zoned mangroves on the tidal flat, and tidal creek incising the tidal flat. **2B:** Spit that has encroached into a mangrove forest, perturbing the zonation; King Sound. **2C:** Shore-parallel dune belt retreating inland, burying and killing mangroves; Ashburton River delta. **2D:** High-tidal sediment aprons skirting sand islands on the high-tidal flat, and mangrove-fringed tidal creek; Onslow area.

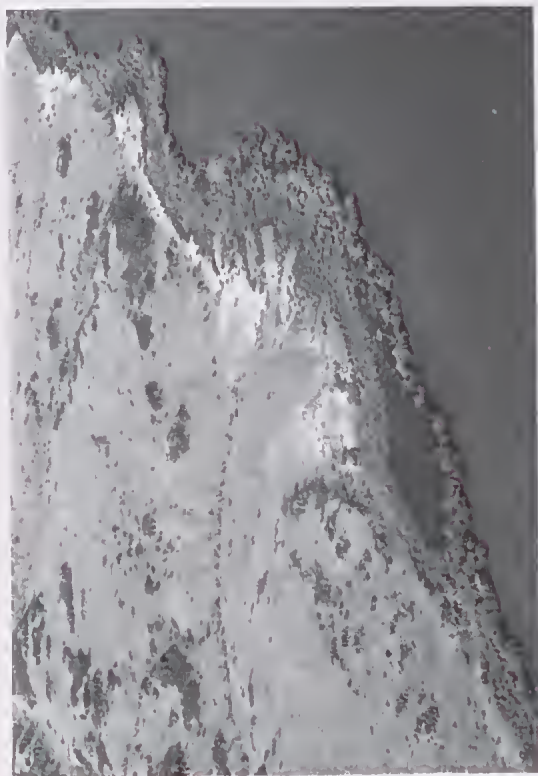
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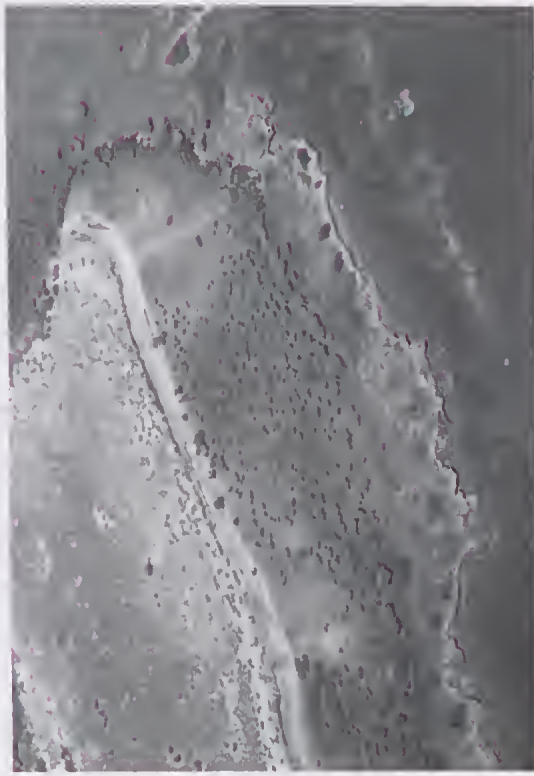
(2G)



(2H)



(2E)



(2F)

Figure 2.—continued 2E: Alluvial fan debouching onto the tidal zone; high tidal part of fan is sparsely vegetated by mangroves, but the mid-high tidal part is thickly vegetated by zoned mangroves; Dampier Archipelago area. 2F: Limestone pavement skirting a limestone island; pavement is sparsely vegetated by mangroves; Thuringa Island, Robe River delta. 2G: Sandstone pavement cut into a sandstone hinterland; pavement is sparsely vegetated by mangroves; Mitchell River, the Kimberleys. 2H: Mangroves inhabiting a small embayment/lagoon; Monte Bello Islands area.

tidal flats, spits, cheniers, rocky shores, limestone pavements, sandstone pavements, alluvial fans, banks of tidal creeks, point bars and shoals of tidal creeks, the hinterland / tidal flat contact, beaches, lagoons, sand islands, and sedimentary aprons skirting sand islands. These habitats are diagrammatically illustrated in Fig 3. Some of these habitats are long-term stable, *e.g.*, rocky shores, alluvial fans, tidal flats, and sand islands, while others are dynamic, *e.g.*, spits, beaches, some tidal creeks. Selected examples of habitats are illustrated in Fig 2 to indicate typical kinds of habitats across a wide range of climatic and coastal setting; features of these habitats are described in more detail in the Figure captions.

For a given climatic region, the main mangrove habitats tend to support a distinct floristic assemblage, or at least a distinctive assemblage identified on both floristics and vegetation structure / physiognomy (Fig 4). Thus for example, a limestone pavement situated between MSL and HWN will support a different floristic and structural / physiognomic assemblage to a muddy or sandy tidal flat located between the same tidal levels. Figure 4, for instance, drawn from Semeniuk & Wurm (1978), illustrates a variety of habitats and their associated mangrove assemblages in the Dampier Archipelago area, with different compositional and physiognomic zonation evident in the different habitats.

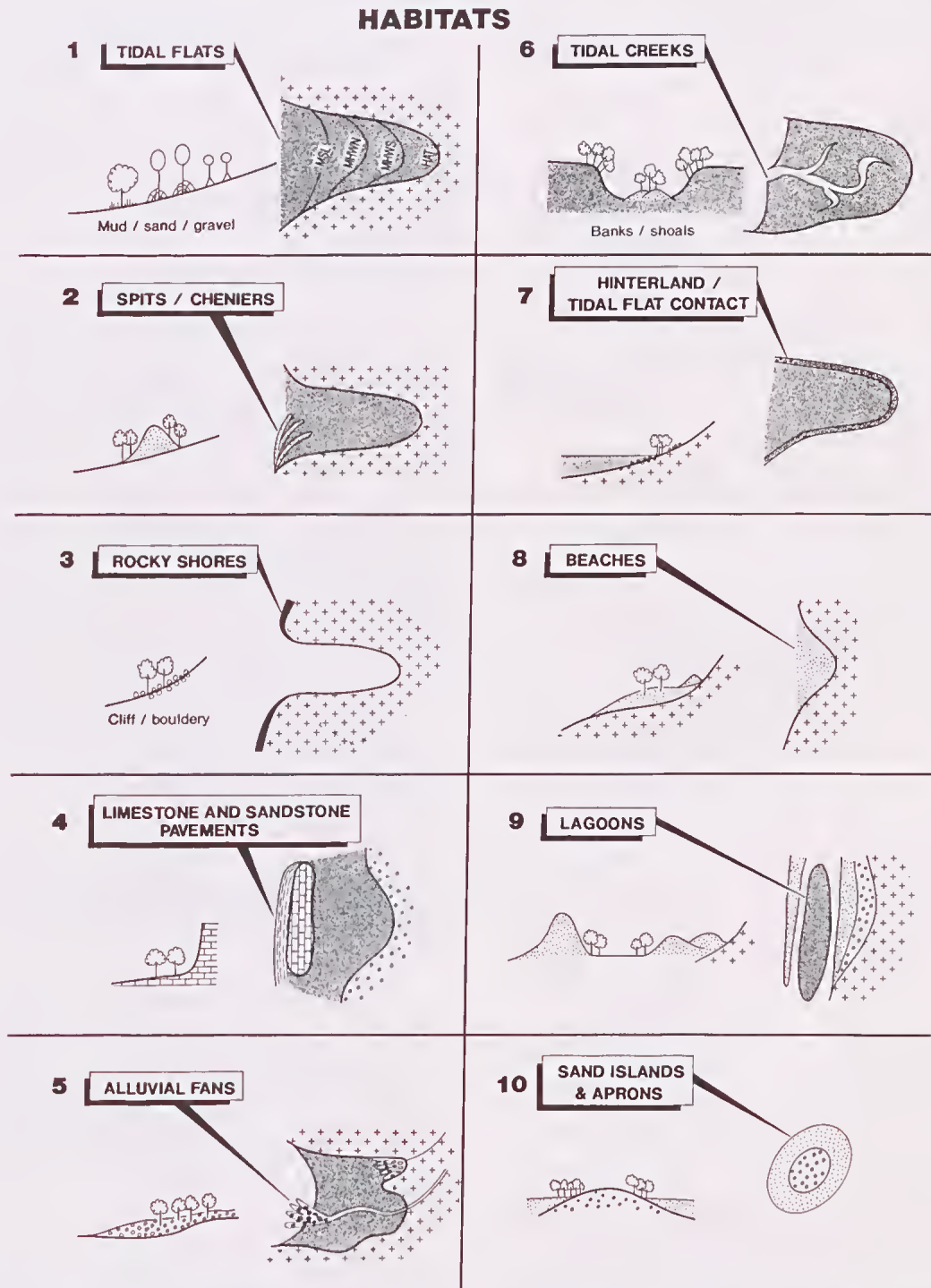


Figure 3. Diagrammatic illustration of the main habitats for mangroves in Western Australia. Each type is illustrated by a plan view and a cross-section, with the location of the mangrove formation within the habitat shown.

Thus for instance, in the Dampier Archipelago area, mangroves exhibit their best physiognomic and composition zonation in the muddy tidal flat and spit (or chenier) habitats; in contrast to those on the muddy tidal flat, mangroves on sandy tidal flats are poorly zoned in terms of composition, but exhibit physiognomic zonation. This aspect of

assemblages related to habitat has been previously investigated by Thom (1967), Thom *et al.* (1975) and Semeniuk (1985). A comparison between similar habitats in different climatic settings also shows that they support different floristic assemblages across the climate zones because the mangroves are drawn from differing species pools (Semeniuk 1985).

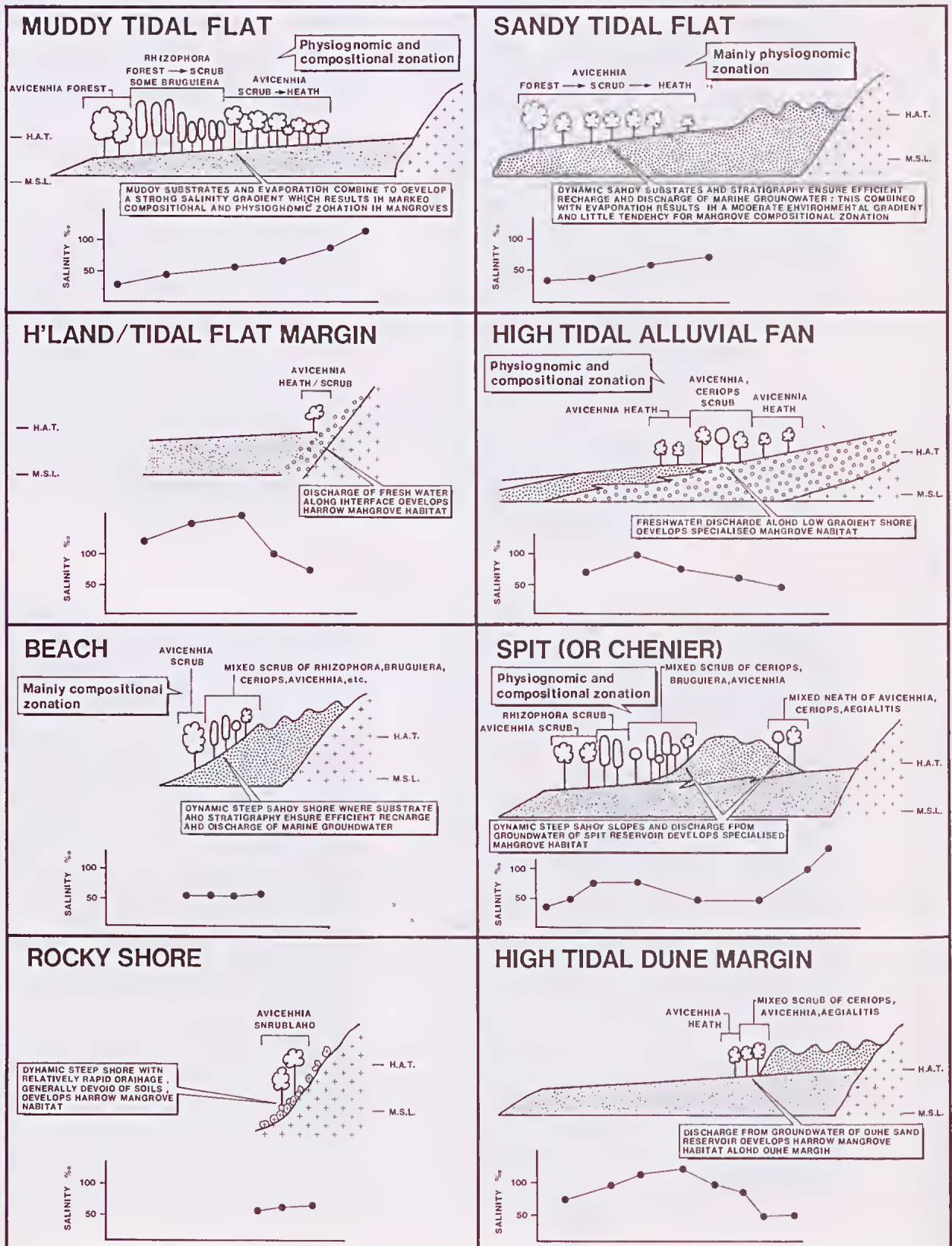


Figure 4. Summary diagram showing key habitat features such as slope, salinity gradients, substrates, and physico-chemical processes, the resulting mangrove composition, structure and physiognomy, and the main processes of maintenance in eight environments in a ria coastal setting in the Dampier Archipelago (after Semeniuk & Wurm 1987).

The study of how habitat types relate to particular mangrove associations (with distinct floristic assemblages or structural/physiognomic types) is the baseline for predicting some of the effects of a sea level rise into heterogenous coastal systems. Within a given climatic region today, the various habitats in a coastal sector support associations of mangroves that are compositionally, structurally or physiognomically related to a specific habitat setting (Fig 4). For example, under conditions of the current sea level position, within a coastal sector in microtidal regime, there may be limestone pavements supporting simple *A. marina* scrub, a muddy tidal flat supporting zoned mangroves (from seaward to landward: *A. marina* forest, *R. stylosa* scrub, and *A. marina* scrub), and a salt flat underlain by limestone pavement. A sea level rise into a system such as this will result in more frequent inundation of the salt flat underlain by limestone pavement so that it will become a MSL-HWN limestone pavement habitat. The current association of simple *A. marina* scrub inhabiting a limestone pavement would indicate that a similar assemblage eventually should inhabit the newly formed limestone pavement after a rise in sea level.

Within each habitat type illustrated in Figure 3, there may be physico-chemical gradients in frequency of inundation, granulometry of substrates, chemistry and mineralogy of the soils, soil moisture, and salinity of soilwater and groundwater, such that there is zonation of mangroves in response to these gradients (cf. Semeniuk 1985, Semeniuk & Wurm 1987).

Mangrove formations in Western Australia are difficult to classify at the large to regional scale because there is much compositional and structural variation due to the mosaics of juxtaposed habitats (cf. Semeniuk 1985, and Semeniuk & Wurm 1987), and zoning induced by physico-chemical gradients within habitats. Elsewhere, mangrove systems, comprising fewer floristic components, have been classified into structural types, e.g., the riverine, basin, fringing and dwarf categories of Lugo & Snedaker (1976) in the Caribbean, but this approach has not been successfully used in Western Australia. The structural schemes (Specht 1981), or floristic schemes (Chapman 1976), used in isolation also are not successful because the former emphasises structure without using floristics, and the latter emphasises floristics without using structure in the nomenclature. The mangrove vegetation unit is a floristic-structural entity, which forms zones or mosaics across a given habitat, and its classification should consider both structural and floristic aspects; a full classification should also involve physiognomic features.

A number of authors have attempted to classify the mangrove formations in Australia (and Western Australia), using varied methods; e.g., mathematical groupings using modern classification techniques (Bunt & Williams 1980), or the Zurich-Montpellier system (Bridgewater 1982), tabular sorting (Bridgewater 1985), structure (Davie 1985), assemblages-linked-to-habitats (Semeniuk 1985), and assemblages-linked-to-habitats at a first level followed by floristic-structural for units within habitat-related assemblages (Semeniuk & Wurm 1987).

The system for classifying mangroves in Western Australia at a primary level according to habitat as proposed by Semeniuk (1985) and Semeniuk & Wurm (1987) is adopted here. This approach names an assemblage after the habitat

in which it occurs. Thereafter it assumes that, as there are physio-chemical variations in the habitat, structural and floristic gradation and zonation of mangroves will occur. According to this approach, the main mangrove assemblages recognised are: 1. muddy tidal flat; 2. sandy tidal flat; 3. gravelly tidal flat; 4. spit/chenier; 5. rocky shore; 6. limestone and sandstone pavement; 7. alluvial fan; 8. tidal creek bank; 9. tidal creek shoal (or point bar); 10. hinterland fringe; 11. beach; 12. lagoon; and 13. sand islands and apron.

Some of these types are specific to certain of the larger scale geomorphic settings, whereas others occur throughout tropical Western Australia. Figure 4 illustrates the type of structure and composition of selected examples of these mangrove assemblages in the Dampier Archipelago area, viz., muddy tidal flat, sandy tidal flat, spit/chenier, rocky shore, alluvial fan, hinterland fringe (colonising the hinterland/tidal flat margin), and beach.

In addition to variation in habitats both locally and regionally, there is compositional (floristic) variation regionally in response to climate. Thus, the floristic assemblages that colonise similar habitats will vary from region to region. Mangrove formations and zones within a habitat may be further classified by floristics and structure at a secondary level (cf. Semeniuk & Wurm 1987); individual zones within assemblages thus may be classified using the schemes of Bunt & Williams (1980), those used by Bridgewater (1982, 1985), or those used by Semeniuk & Wurm (1987).

Coastal sectors for mangrove systems in Western Australia

The tropical coast of Western Australia can be subdivided into sectors of coastal types as a basis for recognising the smaller settings for mangroves in this area. The four main features that determine location and nature of the sectors are (Fig 5): the style and amount of fluvial input from the hinterland to the coastal zone, the mineralogical nature of mud in the mangrove environment, the climatic setting of the coast, and the nature of the oceanographic regime that receives the sediment.

In relation to the style and amount of fluvial delivery of sediment from the hinterland to the coastal zone, six systems are recognised:

- the shoreline of the Kimberley Plateau region, where a series of short rivers drain an uplifted plateau in a humid to semi-arid climate; the coast abuts the edge of the plateau; sediment input is not a major factor in coastal development, but sediment delivery is terrigenous material;
- the large funnel-shaped King Sound and Cambridge Gulf, formed where the post-glacial marine transgression has inundated large valley tracts developed by a series of major rivers in the region; these rivers have cut valleys along major geological contacts; the riverine tracts occur today in a semi-arid climate; sediment input is a major factor in Holocene coastal accretion, and sediment delivery is terrigenous material;
- the shoreline of the seaward edge of the Great Sandy Desert (Canning Basin), where there is negligible to no

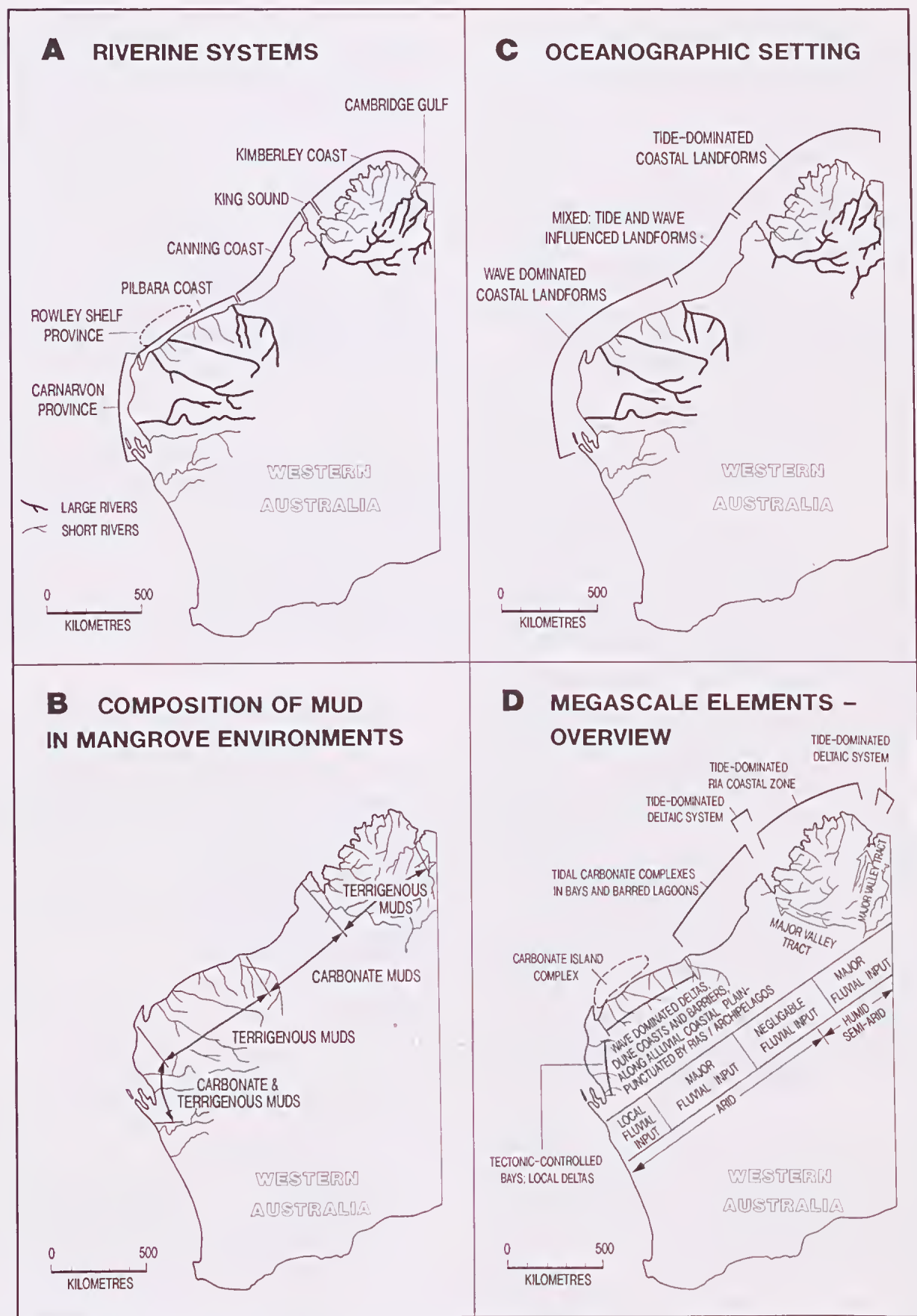


Figure 5. Background information relevant to the coastal sectors in northwestern Australia. **5A:** The riverine systems, showing the large and short rivers in the systems. **5B:** The composition of mud in mangrove environments. **5C:** The oceanographic setting, ranging from wave-dominated in the south to tide-dominated in the north. **5D:** The overview of the coast of northwestern and mid-western Australia showing the important elements of riverine setting, oceanographic setting, composition of mud, and resultant coastal features at the megascale.

fluvial delivery to the coast, and the fine-grained coastal sediment is predominantly carbonate;

- the coast of the Pilbara region where a series of large to medium-sized rivers drain an inland high-relief hinterland in an arid climate and have built a broad, low coastal plain; sediment input is not a major factor in the Holocene, but over the full period of the Quaternary, it has been a major factor in developing the coast; sediment delivery is terrigenous material;
- the system of the oceanic islands offshore from the Pilbara coast; suspended mud from river floods reach these oceanic islands to accumulate in protected areas; sediment input is not a major factor; sediment delivery is terrigenous material; the system of the tectonically complex Carnarvon Basin area where large rivers drain the arid Pilbara uplands and discharge into barred lagoons or into the marine environment; there is a mix of fluvial input and locally derived carbonate sediment, dependant on whether the local system is supplied with or starved of fluvial sediment.

In relationship to the mineralogy of mud found in the mangrove environment, three types are recognised:

- those coasts that are comprised dominantly of terrigenous mud, composed of kaolin and quartz clay and silt, with minor or subordinate amounts of locally derived carbonate mud; these areas are downstream from the zones of major fluvial systems—they are the coastal zones downstream from the Kimberley and Pilbara regions, and include the offshore islands that receive mud in suspension from the the Pilbara river floods;
- a coast that is comprised dominantly of carbonate mud; being starved of all but very minor fluvial sources, there is no opportunity to deliver significant terrigenous mud to the shore; this system comprises the shoreline of the Canning region;
- a system that is mixed: some parts are of terrigenous mud, where rivers have breached to the coast, and some dominantly of carbonate mud; this system is within the tectonically active Carnarvon Basin.

In regards to climate, there are three types of settings:

- a humid to subhumid climate in the Kimberley region; a semi-arid climate in the area of King Sound, Cambridge Gulf, and part of the Canning region; an arid climate in the Pilbara, the oceanic island system, and the Carnarvon region.

In relationship to oceanography, there are three types of systems:

- a tide-dominated system, with macrotides in King Sound, Cambridge Gulf, and the Kimberley region; in this system deltas are tide-dominated forms;
- a mixed tide-influenced and wave-influenced system along the coast of the Canning region, where the tidal regime is macrotidal, but wave processes are still effective in developing coastal landforms;
- a wave-dominated area, but within which the tide regime varies from microtidal in the south to macrotidal in the north, in the Pilbara, the oceanic islands system on the Rowley Shelf, and the Carnarvon region; deltas in these systems are wave-dominated forms.

In combination, these regional features develop seven coastal sectors. From north to south, these sectors and a summary of mangrove habitats within them are (Figs 6 & 7):

1. **Cambridge Gulf**, with mangrove habitats in a tide-dominated deltaic-estuarine environment in a gulf setting where the mud component of the sediments is dominantly terrigenous;
2. **Kimberley Coast**, with mangrove habitats in a tide-dominated ria-archipelago setting where terrigenous mud is dominant where the mud component of the sediments is dominantly terrigenous;
3. **King Sound**, with mangrove habitats in a tide-dominated deltaic-estuarine environment in a gulf setting where the mud component of the sediments is dominantly terrigenous;
4. **Canning Coast**, with mangrove habitats in a barred to open tidal embayment settings where the mud component of the sediments is dominantly carbonate;
5. **Pilbara Coast**, with mangrove habitats in wave-dominated settings of deltas, beach/dune coasts, limestone barrier islands, and ria-archipelago shores; the mud component of the sediments is dominantly terrigenous;
6. **Rowley Shelf Province**, with mangrove habitats in small embayments along the wave-dominated island shores and in lagoons of the island interiors; the mud component of the sediments is dominantly terrigenous; and
7. **Carnarvon Province**, of uplifted Tertiary rocks, with mangrove habitats along the coast in small embayments, lagoons, and wave-dominated deltas, and inland in saline playas; the mud component of the sediments is dominantly terrigenous or carbonate, dependant on setting.

COASTAL SECTORS FOR MANGROVES

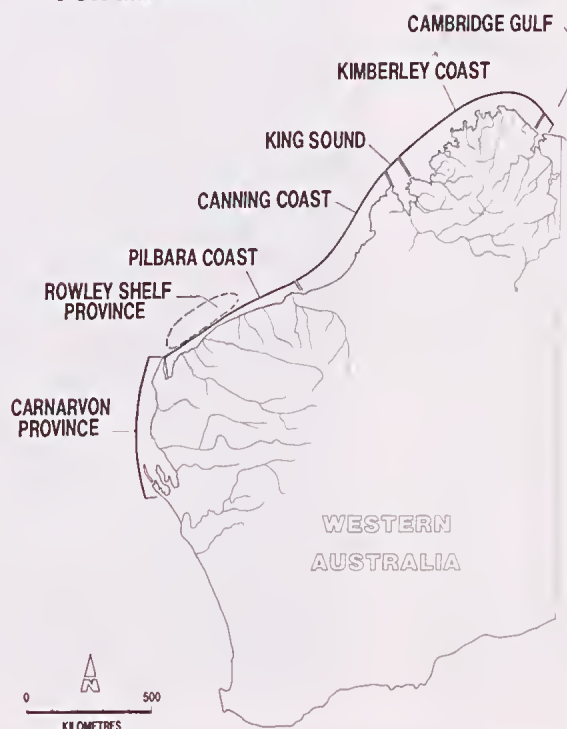


Figure 6. Coastal sectors for mangrove systems in northwestern Australia, from information presented in Fig 5D.

MANGROVE HABITATS AND STYLE OF MANGROVE SYSTEMS WITHIN COASTAL SECTORS

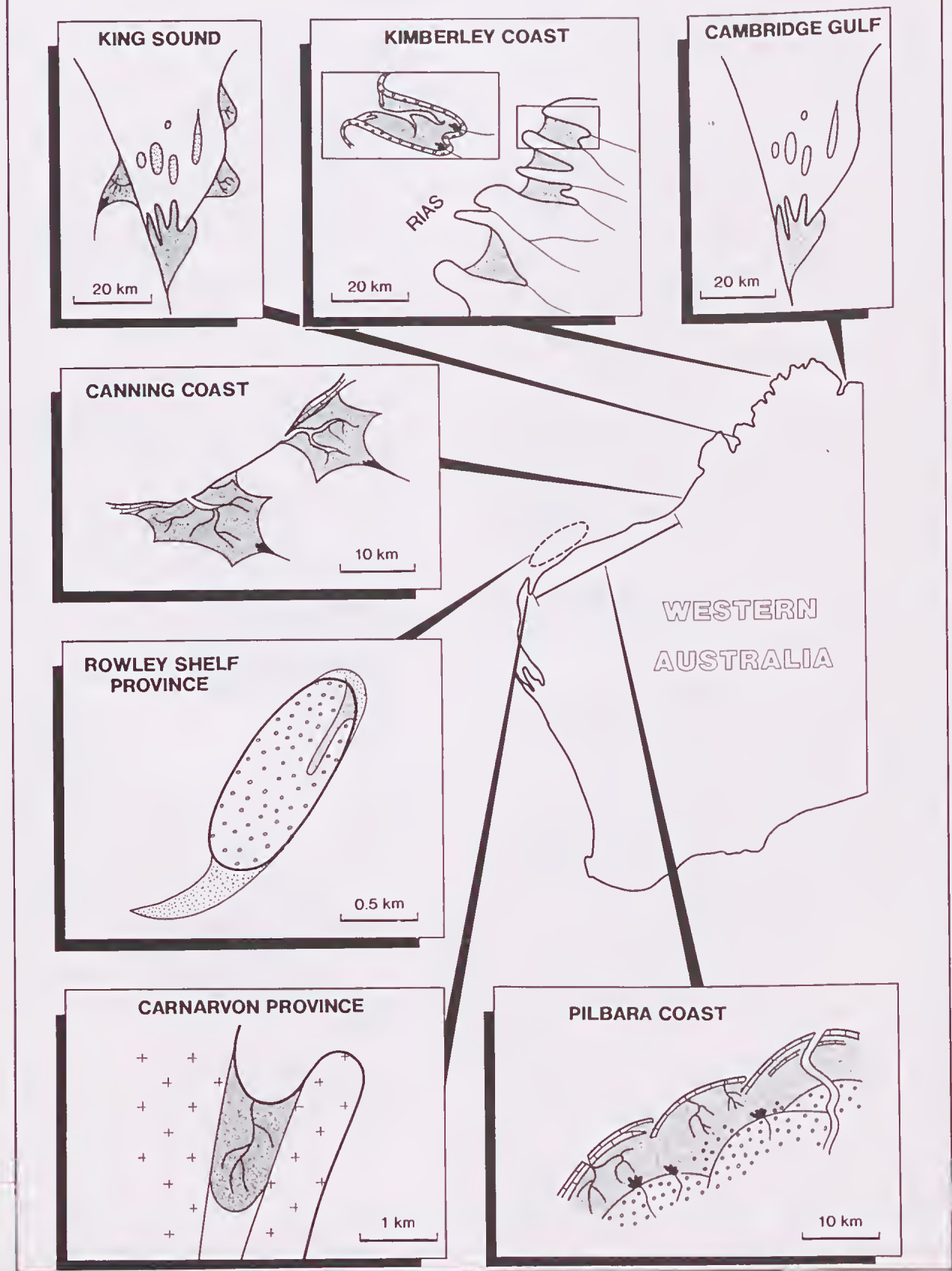


Figure 7. Summary of mangrove habitats and style of mangrove systems within the coastal sectors. Each coastal sector has a distinct style of coastal form and distinct suites of mangrove habitats as discussed in the text.

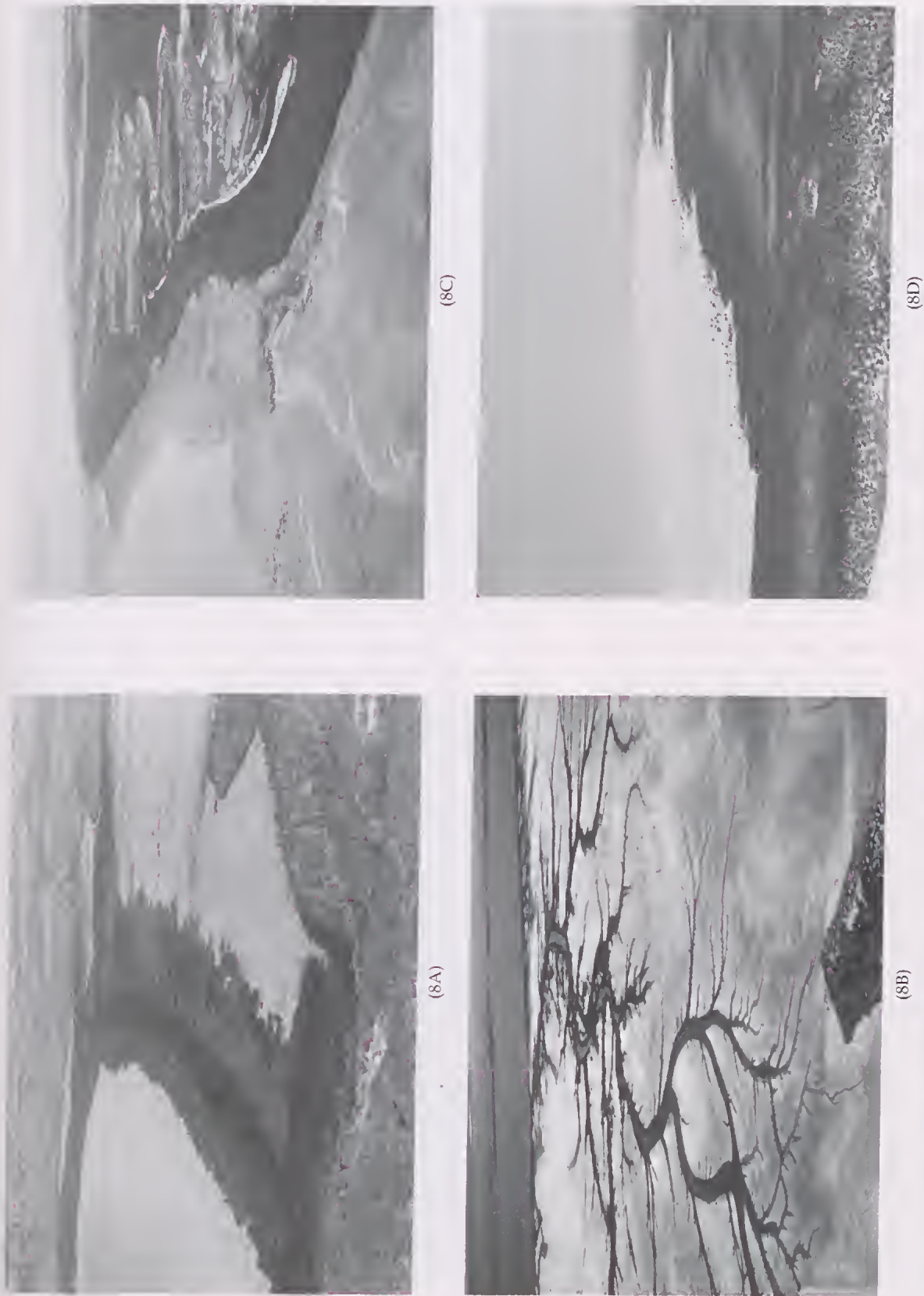
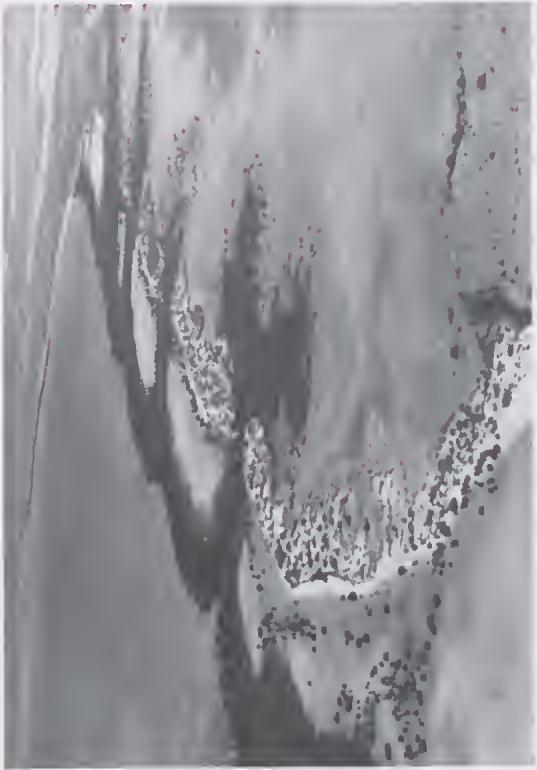


Figure 8. Aerial photographs showing typical views of mangrove systems in the coastal sectors, proceeding from the Kimberley Coast in the north to the Carnarvon Province in the south, to illustrate the variation in mangrove systems within each of the coastal sectors. 8A: Zoned mangrove on tidal flat, Port Warrender area, the Kimberley Coast; salt flat landward of the mangroves, and a hinterland fringe of mangrove are also evident. 8B: Mangrove-fringed tidal creek traversing a broad salt flat, King Sound. 8C: Coast cut into a linear dune field to develop spits from the dune tips; mangroves fringe the coast in front of eroding spit line; King Sound. 8D: Simple mangrove formation of *Avicennia marina* inhabiting broad tidal embayment; white nature of carbonate tidal mud is evident; Roebuck Bay, Canning Coast.

Figure 8 continued overleaf . . .



(8E)



(8G)



(8F)



(8H)

Figure 8.—continued 8E: Limestone barrier fringed by mangrove; Yammedary Island, Pilbara Coast; 8F: Tidal creeks meandering through mangrove vegetation; Weld Island area, Pilbara Coast; 8G: Mangroves lining the coast, succeeded to landward by a line of cheniers and further to landward by a salt flat; tidal creek headwaters incise into the line of cheniers; Regnard Bay area, Pilbara Coast. 8H: Mangroves inhabiting depressions between beach ridges, Gascoyne delta, Carnarvon Coast (photograph: D P Johnson).

Each of the coastal sectors has a distinct range of large-scale coastal landforms, and local geomorphic and sedimentary patterns (Figs 7 & 8). Within the coast types there also are a profusion of smaller-scale habitats, the scale at which mangrove populations respond; these may be restricted to, and distinctive of a particular setting. Figure 7 illustrates for each of the coastal sectors, the style of mangrove habitats present within them. Thus, for instance, King Sound and Cambridge Gulf are both large funnel-shaped embayments within which tide-dominated coastal features are evident. The Canning Coast is composed of small embayments that are incised by tidal creeks and semi-barred by spits or limestone ridges. The Pilbara Coast is a complex of deltas, barrier islands, older Pleistocene deltas and local alluvial fans, with incision of the system by tidal creeks. The small islands set in the Rowley Shelf system have, along their periphery, spits, small lagoons and beaches developed as mangrove habitats. In parts of the Carnarvon Province, mangrove habitats are developed in embayments between tectonically uplifted bedrock ridges. Figure 8 exhibits some typical views of the various coastal sectors, proceeding systematically from the Kimberley Coast to the Carnarvon Province, to illustrate the variability of the mangrove systems.

A brief description of the sectors in terms of their geological setting, the dominant processes therein, and the range of small-scale mangrove habitats is presented below. Tidal information for the different locations is from Calder (1979).

Cambridge Gulf Cambridge Gulf is a large gulf with a tide-dominated delta at its head (Thom *et al.* 1975), that has a semi-arid climate. It is located along the structural edge of the Kimberley Block, and is a marine-inundated valley tract that has been scoured out by large rivers of the region. The hinterland is composed of uplifted Precambrian sedimentary rocks flanked by aprons of alluvium. The tidal deposits that partly fill the gulf are sand overlain by mud. Tides are semidiurnal and macrotidal, with a mean spring tidal range of 6.6 m (Wyndham), and a maximum range of 9.1 m. The system is tide-dominated, but the large fetch of the north-south oriented gulf results in the generation of local wind waves that effect sand transport and the building of wave-built features such as spits and cheniers. Periodic storms also result in the building of cheniers that face the direction of the large fetch (Thom *et al.* 1975). Within this system, the mangrove habitats are broad tidal flats, spit/chenier systems, and large-scale to small-scale tidal creek banks and associated sediment islands and shoals (Thom *et al.* 1975).

Kimberley Coast The Kimberley Coast fringes the dissected Kimberley Plateau which is composed of uplifted Precambrian rock. The area is set in a subhumid to humid environment. Tides are semidiurnal and macrotidal, with a mean spring tidal range of 6.4 m and a maximum range of 8.6 m (Port Warrender). The coastal system has formed by marine flooding of the dissected hinterland to develop a steeply indented shore and island complexes. As such, there is an inter-gradational range of ria shores and archipelagos. At the regional scale, the Kimberley coast shows the following coastal types: ria coasts, with narrow embayments, broad embayments, straight coasts and islands; tidal-land connected islands; and archipelagos, whose margins have the same suite of units as ria coasts; sediments fill the head of ria embayments, but the outer parts of the rias are largely

sediment-depauperate. Tidal sediments filling the embayments and rias are sand overlain by mud, or locally totally mud (Semeniuk 1983, 1985). Within the various large-scale embayments there is a recurring suite of mangrove habitats including tidal flats, tidal creeks, spits, alluvial fans, rocky shores and hinterland margins (Semeniuk 1985), and locally, sandstone (tidal) pavements (Figs 2A, G, Fig 8A).

King Sound King Sound, comprised of the Fitzroy River estuary and Stokes Bay, is a large gulf with a tide-dominated delta at its head (Jennings & Bird 1967; Jennings 1975; Semeniuk 1981a), similar to Cambridge Gulf. The area has a semi-arid climate. Tides are semidiurnal and macrotidal, with a mean spring tidal range of 9.8 m and a maximum range of 11.5 m (Derby). The gulf is a marine-flooded former broad valley scoured out by large rivers which have selectively eroded the structural junction between Precambrian and Mesozoic rocks. The hinterland immediately surrounding King Sound is mainly of Mesozoic rock overlain by Quaternary linear dunes, but the northern boundary is of Precambrian rock.

The system is tide-dominated, and as in Cambridge Gulf, the large fetch of the north-south oriented gulf results in the generation of local wind waves that effect sand transport and the building of wave-built features such as spits and cheniers. Periodic storms also result in the building of spits and cheniers that face the direction of the large fetch. Holocene tidal deposits that partly fill the gulf are sand overlain by mud (Semeniuk, 1981b), and these truncate and overlie the linear dune system (Jennings 1975). Most of the tidal land in this area is eroding on a large scale (Jennings 1975, Semeniuk, 1981a), and the various coastal features in the King Sound are products of this process. In northern areas the dune fields are truncated and develop spits along the erosion line (Fig 8C). The tidal zones of King Sound have been classed according to geomorphology into 7 types (Semeniuk, 1981a): depositional flats, unconformity flats, shoal flats, spit/chenier flats, rocky shores, mid-gulf shoals and islands. These units also form the basis of the main mangrove habitats in this sector, which include broad tidal flats, spits (Fig 2B) and cheniers, large-scale to small-scale tidal creek systems (Fig 8B) and associated shoals. Much of the mangrove zonation is related to the style of erosion along the coast, since erosion determines the type of geomorphic surface (Semeniuk 1980a).

Canning Coast The Canning Coast sector is the shore cut into the Canning Basin and it forms the seaward edge of the Great Sandy Desert. This sector has a semi-arid climate. Tides are semidiurnal and macrotidal, with a mean spring tidal range of 8.2 m and a maximum range of 11.0 m (Broome). Although the system is macrotidal, the coastal regime is both wave- and tide-influenced. Wind is an important factor in coastal processes in that it is responsible for developing dune coasts, and wave-developed coastal landforms such as spits that emanate from headlands.

In terms of sediment types, the important feature of this sector is that there are no major river outlets into the marine environment, and little or no fluvial run-off from a predominantly desert dune hinterland. Hence mud derived from terrestrial sources is negligible, and carbonate mud on tidal flats is characteristic of the sector. The settings of the mangrove habitats in this area have formed mainly by pre-Holocene processes: erosion of Mesozoic rock and Cenozoic

aeolian hinterland has formed shallow valleys, and these have developed into a series of scalloped embayments now partly filled with mud and vegetated by mangroves. Locally, barrier spits and dunes have formed at the headlands of the embayments. Headwaters of the embayments receive some fluvial sediment which locally accumulates as sandy alluvial fans. Erosion is currently dominant in this sector, and all the mud-filled embayments have been trimmed back to expose the bedrock of their flanking headlands.

The Canning Coast between Cape Bossut and Cape Leveque exhibits a recurring geomorphic pattern of open bays and bays barred by dunes and ridges. The suite of coastal types are:

- large scale "v-shaped" bays, with smaller "v-shaped" margins; these bays are comprised of carbonate mud in upper tidal parts and sand in lower tidal parts;
- a system or series of Quaternary (Pleistocene to Holocene) sandy or limestone barriers, beach ridges, and spits, usually along the southern/southwestern portion of large scale bays—these result in the formation of a southern shore complex consisting of an "en echelon" series of smaller barred embayments (which are similar to the large-scale bays in terms of geometry and sediment systems); and
- scalloped, "v-shaped" interfaces between the high tidal zone and the hinterland.

The reasons for these recurring patterns are the "basement" geological control of disposition of headlands and their associated embayments, the regional oceanographic processes that resulted in longshore (generally northward) sediment transport, the formation of Quaternary barrier structures that emanate from headlands and protruding sections of the sandy hinterland (these barriers then shelter smaller bays and lagoons), and ancestral drainage lines—these are truncated at their seaward edge by the shore, but continue to function as sites of discharge of freshwater and alluvial sediment to tidal flats.

Eighty Mile Beach is part of this sector. Although there are no mangroves along the seafront there, mangrove mud is locally exposed along the eroding beach-face indicating that the coastal dune barriers are retreating over former mangrove environments/ deposits, and that the extent of mangrove along this portion of coast was greater earlier in the Holocene. Inland from this coast is *A. marina* as reported by Beard (1967).

Tidal flats in the region are of two types: sand-dominated flats that occur on the open coasts, and mud-dominated flats that occur typically in the various bays. Mangroves are best developed in the embayment settings (Fig 8D), and inhabit tidal flats, tidal creek systems, local spits, and (stranded) inland depressions and creeks.

Pilbara Coast The Pilbara Coast is the most varied of mangrove coasts in northwestern Australia. The unifying feature of this coastal sector is that it is a sedimentary repository for a range of rivers that drain a high-relief Precambrian rocky hinterland. The rivers discharge sediments along a coastal plain (the Abydos, Onslow and Yannarie coastal plains; Beard, 1975) that fronts a wave-

dominated environment in an arid climate. The combination of fluvial and shoreline accretion processes, coastal cementation, coastal erosion, and ancestral landform architecture (such as residual limestone ridges and large outcrops of Precambrian bedrock) inherited from the Pleistocene and older periods, has produced a laterally heterogeneous coastal system (Semeniuk 1993).

Prevailing winds develop coastal dunes, and influence the construction of coastal sediment bodies by wind waves (Semeniuk & Wurm, 1987). Cyclones are common (Coleman 1971, Milton 1978; Lourenz, 1981), causing flash flooding, marked river discharge of sediment into the coastal plain, accumulation of spits in the coastal zone, and erosion and dispersion of coastal sediment bodies. Long-period swell, local wind waves, landbreeze/seabreeze systems and thunderstorms contribute to develop wave-dominated coastal landforms such as deltas, beaches, spits and bouldery shores (Steedman, 1985; Steedman & Colman 1985; Semeniuk, 1985; Semeniuk & Wurm, 1987). Tides along the Pilbara coast are semi-diurnal, with mean spring tidal ranges varying (south to north, i.e., Onslow to Port Hedland) from 1.8 m to 5.8 m, and maximum tidal ranges varying from 2.8 m to 7.8 m (Easton 1970).

The Pilbara coastline is dominated by deltas, barrier coasts associated with inactive deltas, limestone barrier coasts and their associated protected lagoons and embayments, intervening bays formed where barriers have eroded to expose the formerly protected mud-floored lagoons, and archipelago-ria shores. Within these there is a multitude of varied large-, medium- and small-scale coastal landforms and sedimentary deposits such as limestone islands/barriers, spits, cheniers, sand mounds and shoals, sand aprons around islands, alluvial fans, tidal creeks, etc, often specific to a particular coastal setting (Figs 2D, E, F, Fig 8E, F, G).

Wave-dominated, active deltas occur in discrete locations in this region. Within the deltas are prodelta sediment veneers, delta front sand flats, shoals and spits, plains of shore-parallel sand ridges, strandplains with mangrove-vegetated mud-floored lagoons, mud flats with cheniers, systems of active to inactive channels, gravel flats and gravel ridges, and wide, extensive high-tidal plains, underlain by mud, which become hypersaline salt flats. Beach/dune shores are composed of beaches, beach ridges, high relief sand dunes, mobile crescentic dunes on the tops of the dune plain, interdune swales and linear, mangrove-vegetated, mud-veneered depressions, and mangrove-lined inlets formed by tidal creek erosion of the dune belt. Inactive eroding deltas, and their barriers, combine the elements of active deltas and of beach/dune shores, with the result that barriers of limestone, or gravel ridges, or sandy ridges often are laterally associated with, or form the seafront to them. As with the active deltas, the delta plain in these systems commonly is a high-tidal mud flat, or locally a sand flat, which becomes an extensive hypersaline salt flat.

Limestone barrier coasts have prominent ridges of Pleistocene limestone forming a shore-parallel barrier (or barriers) protecting muddy embayments/lagoons that are dissected by tidal creeks and vegetated by mangroves. Erosion is dominant here, with sea-front erosion of the barriers, tidal creek erosion of mud deposits leeward of barriers, and salt weathering in high-tidal environments. Limestone barriers

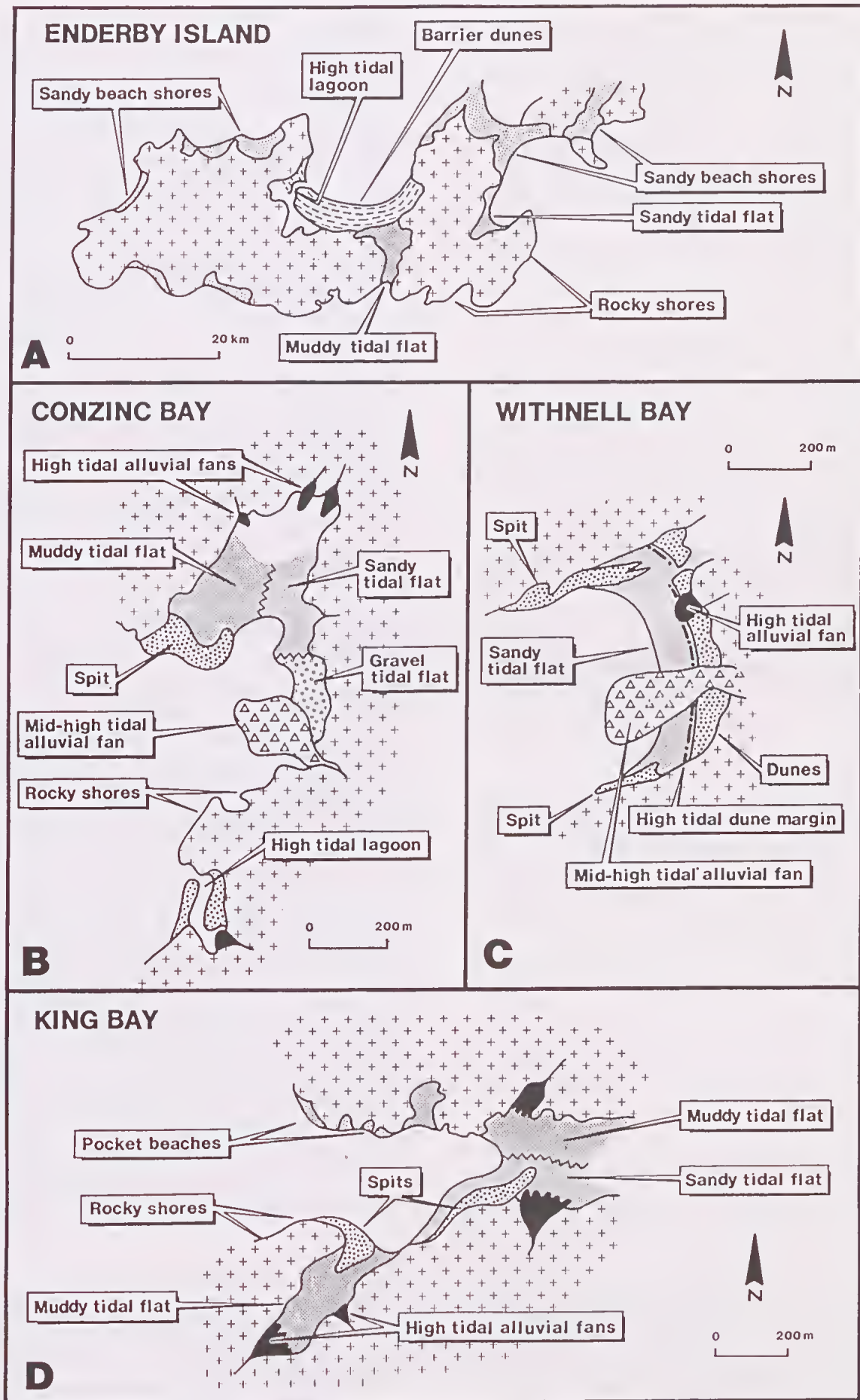


Figure 9. Examples of mangrove habitats in the ria/archipelago setting of the Dampier Archipelago (after Semeniuk & Wurm 1987). In this heterogeneous coast, the recurring pattern of muddy and sandy tidal flats, alluvial fans, spits and beaches are evident. The heterogeneous array of habitats results in a heterogeneous array of mangrove assemblages.

erode to the extent that they expose the leeward mud deposits to form eroding mud coasts fringed at the seafront by mangroves, extensive hypersaline salt flats (*i.e.*, the high-tidal surface of the former embayment), and mangrove-fringed tidal creeks.

Archipelago/ria coasts occur where Precambrian bedrock crops out at the shore. Fracture patterns and disposition of resistant rocks determine the orientation and location of valleys and ridges of the pre-Quaternary topography (Semeniuk *et al.* 1982). Marine inundation of this terrain has formed a gradational suite of isolated scattered small islands, islands interconnected by tidal lands of sand or mud, and dissected large islands that retain "rias" along their margins. Mangrove environments in this setting include tidal flats, spits, beaches, dunes, tidal creeks, rocky/bouldery shores, high tidal alluvial fans, and sediment aprons along the upland margin (Fig 9; Semeniuk & Wurm 1987).

A number of causative factors contribute to the development of regional scale coastal types in the Pilbara system. Most of the coast has been built by a combination of deltaic and alluvial fan accretion, alternating with coastal retreat/erosion that either has built barriers or has developed scalloped bays. This pattern has been built around and upon extensions of hinterland bedrock outcrops. The main causative factors are:

- fluvial construction to develop alluvial fans and delta lands along the broad margin of the Pilbara uplands; this has been the main factor in building the coastal plain;
- destruction of deltas to develop barrier coasts and associated bays;
- longshore transport away from active deltas, and onshore aeolian activity, concomitant with delta land construction, to build coastal dune belts;
- Pleistocene limestone barrier ridges formed as aeolian accumulations along former shorelines, or formed by destruction of Pleistocene deltas;
- continuing coastal erosion to remove limestone ridges of barrier coasts and to develop scalloped, embayed coasts; and
- outcrops of Precambrian bedrock, extending from the hinterland into the coastal zone, to form archipelagos and scattered islands.

These coastal processes and features occur in different parts of the Pilbara Coast. For example, the Turner, Maitland and De Grey rivers have built active deltas, and bedrock outcrop forms the Dampier Archipelago and the Point Sampson—Cossack area (Semeniuk *et al.* 1982; Semeniuk & Wurm 1987). The barrier coasts and deltas are intergradational (since deltas with wave destruction develop into barrier systems), and this intergradational suite forms the predominant seafront architecture of the Pilbara Coast. Thus the Pilbara Coast can be viewed as a coastal plain of alluvial and tidal flat sediments, with a system of nearly continuous stretches of limestone and Holocene dune barriers, behind which are protected embayments, lagoons and tidal flats. This prevalent pattern is disrupted locally by deltas, or by bedrock outcrops.

Rowley Shelf Province The islands of the Northwest Shelf between Exmouth Gulf and Dampier Archipelago comprise the Rowley Shelf Province. They occur in an arid, oceanic setting. Tides are semidiurnal with a mean spring tidal range of 2.5 m and a maximum range of 3.6 m (Barrow Island). Five types of islands are recognised: Tertiary limestone island(s); Pleistocene oolitic limestone islands; Pleistocene aeolianite limestone islands; Holocene sand islands; and residuals of eroding deltas. The shoreline of islands tends to be armoured with beach rock formation that stabilises the islands against erosion. Local small embayments, lagoons, sheltered beach bays, sites leeward of spits, depressions interior to the islands, and limestone pavements constitute the main mangrove habitats in this system.

Carnarvon Province The Carnarvon Province is part of the modern Carnarvon Basin (Logan *et al.* 1970; Geological Survey of Western Australia 1975) and is set in an arid climate. This system contains mangrove environments in coastal and inland settings, with the majority of mangroves in the coastal settings. The coast of this province is microtidal with mean spring tidal ranges of 2.1 m and 0.9 m and maximum ranges of 3.0 m and 1.4 m recorded at Learmonth and Carnarvon, respectively. Most of the coast is wave-dominated.

This sector exhibits considerable heterogeneity because of its strong tectonic history in the Cenozoic. North-trending uplifted anticlinal structures, composed of Tertiary sedimentary rocks, are common in the region, and as a result, there is a complicated array of ridges and local uplands, separated by lowlands and grabens. One of the prominent depositional lowlands is termed the Bullara Sunkland (Logan *et al.* 1970) and is the site for the Shark Bay system, Lake Macleod and part of Exmouth Gulf. The ridges of uplifted rock influence the location of depositional basins (grabens), coastal bays, and the position of peninsulas, barriers and capes. Tectonic uplift also has diverted a number of rivers which now drain into a barred megascale lake (Logan 1987). Only two rivers reach the sea to form deltas: the Gascoyne delta (Johnson 1982) and the Wooramel delta. In the Carnarvon Province, mangrove environments occur in different systems dependant on their geologic/tectonic setting: in small to large, protected to sheltered embayments cradled by the anticline structures where the geological grain of the uplift intersects the coast (Brown 1976, 1988; Fig 7); in delta settings; in inland coastal basins (Lake Macleod); in small inland depressions; and at the landward edge of prograded seagrass bank systems in front of the Pleistocene Boodalia delta (Davies 1970). Within these settings, the mangroves colonise tidal flats, tidal creeks, margins of spits, borders of lagoons, and the strandplains within the delta.

Boundaries between the coastal sectors

The nature of the boundaries and their relationship to geologic framework is only discussed here for the mainland sectors. The Rowley Shelf Province which stands clearly alone and distinct does not need clarification.

The boundaries between Cambridge Gulf and the Kimberley Coast, and between King Sound and the Kimberley coast are sharp and related to major boundaries in the

geological systems. The boundary between the Canning Coast and King Sound is sharp and related to the shape of the gulf of King Sound, the influence of the Fitzroy River sediments, and the course of the Fitzroy River system. The boundary of the Canning Coast and the Pilbara Coast also is sharp; the Pilbara system begins with the first appearance of the Pilbara rivers (the De Grey) that brings with it to the coast terrigenous sands and muds; the first embayment (Cape Keraudren area) to the northeast of this river is a carbonate mud system.

The boundary of the Pilbara Coast with the Carnarvon Province requires further discussion. This boundary is placed at the southern centre of Exmouth Gulf where the last prominent ridge (Giralia Anticline; Logan *et al.* 1970) crops out to influence coastal topography: to the west of this ridge is the western shore of Cape Range with its system of mangrove-vegetated bays and lagoons, and to the east are broad mangrove-vegetated tidal flats (Yanrey Flats; Brown 1976). To the northeast of this ridge, the prominent tectonic terrain of the Carnarvon Province is subdued and buried by sediments of the coastal plain ribbon (Yannarie Coastal Plain; Beard 1975) of the Pilbara. Thus Exmouth Gulf is not viewed as an independent system for mangroves (*cf.* Semeniuk 1986b), but rather as a geographic gulf that straddles two separate coastal systems. The eastern shore of Exmouth Gulf, *i.e.*, Yanrey Flats, is grouped with the Pilbara Coast rather than within an "Exmouth Gulf system" because it forms the seaward edge of the Yanrey and Ashburton river drainages. The Yanrey Flats actually are contiguous with, and indistinguishable from the flats associated with the Ashburton and Cane rivers, and on this basis alone should be considered as part of the Pilbara Coast. Three additional features support this grouping. Firstly, the headwaters of the Yanrey River drain the rocky terrain of the Pilbara uplands (Geological Survey of Western Australia 1975), and has the morphology of a typical Pilbara river. Accordingly, the coastal part of this river should be grouped with other Pilbara rivers. The next river south of the Yanrey is diverted by the tectonics of the Carnarvon Province and empties into the north of Lake Macleod. Secondly, while the Yanrey River channel does not enter the sea with a conspicuous river mouth, as do the other prominent Pilbara rivers, examination of the delta lowlands reveals that the main channel of the Yanrey River bifurcates into numerous small channels that wind their way through, and locally are absorbed by, dune fields. The delta distributary channels *are* present, but are more diffuse and dissipated. Thirdly, the eastern shore of Exmouth Gulf is broadly lobate between the south-eastern part of Giralia Bay and Talandji (leeward of Tent Island); this lobate form is less pronounced but similar to the seaward margins of the other Pilbara river deltas (*e.g.*, Robe River and Fortescue River deltas).

Relationship to hinterland margin

The various mangroves systems and their habitats occur in clearly defined sectors related to hinterland geology (in part), coastal processes, and sedimentary provinces. The relationship of the hinterland margin to the tidal environment, a feature important in determining how fresh water is discharged into mangrove systems (Semeniuk 1983), also is linked to the sector setting, as the various sectors have differing types of contacts between the hinterland and tidal zone, varying from rock/colluvial, to dune, to limestone

cliff, to alluvial plain (see Semeniuk 1983). For instance, the Kimberley ria coast with its high relief terrain and drainage channels has a variety of geomorphic and stratigraphic units such as alluvial fans and hinterland-margin (colluvium) sheets to facilitate fresh water discharges. The Canning Coast, in contrast, with its low-relief desert dune terrain, internal drainage and tidal embayment habitats, mostly does not contain the geomorphic and stratigraphic features to facilitate fresh water discharge. In addition, these two sectors are set in different climates, such that the availability of hinterland fresh water further contrasts them.

Discussion

The ensuing discussion develops comparisons with previous studies, delineates regions for mangroves in Western Australia, and provides a global significance to the Western Australian mangroves.

Comparisons with previous studies

The tropical coast of Western Australia has been previously described or classified by Jutson (1950), Carrigy & Fairbridge (1954), Davies (1977), Woods (1980), Galloway (1982), Gill (1982), Woods *et al.* (1985) and Semeniuk (1985, 1986a,b). The specific studies dealing with coastal classification, coastal sectors, and the distribution of mangrove habitats at subcontinental to regional scale are Woods (1980), Woods *et al.* (1985), Gill (1982), Galloway (1982), Thom (1982), and Semeniuk (1985, 1986).

Woods (1980) and Woods *et al.* (1985) divided the tropical Western Australian coast into four sectors based on regional geology, but the natural coastal sectors do not always correspond with the boundaries of basement geological units. In the Kimberley Block and the mobile zones that border its eastern and southern margins, the basement geological framework determines the disposition of these coastal sectors, but this is not the case for the boundaries of the natural coastal sector in the Pilbara region. Here the coastal plain (comprised of a sedimentary apron) formed down-stream from the Pilbara uplands. The seaward edge of the laterally continuous plain which forms the basis of the Pilbara coastal sector is comprised of alluvial fans, alluvial plains and deltas, and in fact it overlies three geological units and their contacts, *viz.*, the Pilbara block, the Carnarvon Basin and the Canning Basin.

Gill (1982) identified three sectors in the region of northwestern Australia and also noted their relationship to hinterland geology, but this classification is too simple and does not adequately address the variability of the Western Australian tropical coast.

Galloway (1982) recognised five coastal sectors, termed "mangrove regions", in tropical Western Australia as a framework to describing physiographic patterns of mangrove distribution in Australia generally. From south to north in Western Australia, these units were: Region 1—Northwest Cape to Cape Keraudren; Region 2—Cape Keraudren to Cape Leveque; Region 3—Cape Leveque to Point Osborne; Region 4—Point Osborne to Cape Dussejour; and Region 5—Cape Dussejour to Point Pearce. I am largely in agreement with the location of four of the regions of Galloway (1982),

i.e., the sectors of Cambridge Gulf, Kimberley Coast, King Sound and Canning Coast of this paper coincide with Galloway's regions. However, I do not agree with the Cape Keraudren to Northwest Cape Sector of Galloway, because it agglomerates the entire Pilbara Coast with a portion of the system associated with the western shore of Exmouth Gulf. Galloway (1982) does not recognise the mangroves in the Carnarvon Province as a mangrove region, nor the islands of the Rowley Shelf. The correlation of the coastal sectors as outlined in this paper with those of Galloway (1982) is outlined in Table 2.

Table 2

Comparison of the coastal regions of Galloway (1982) with this study

This study	Galloway (1982)
Cambridge Gulf	part of Cape Dussejour to Point Pearce
Kimberley Coast	Point Osborne to Cape Dussejour
King Sound	Cape Leveque to Point Osborne
Canning Coast	Cape Keraudren to Cape Leveque
Pilbara Coast	part of Northwest Cape to Cape Keraudren
Rowley Shelf	not recognised
Carnarvon Province	not recognised

Thom (1982) outlined five regional-scale types of coast in Australia within which mangroves occur: river-dominated allochthonous systems (mainly deltas); tide-dominated allochthonous systems (mainly deltaic); wave-dominated allochthonous systems (barriers and lagoons); composite river- and wave-dominated systems (of alluvial plains, deltas, and barriers); and drowned bedrock valleys (rias and alluvial plains). Thom (1982) emphasised that allochthonous sediments were brought to the coast to develop coastal landforms as habitat settings for mangroves under conditions that were river-, wave-, or tide-dominated (his Figure 1.1 illustrates the recurring pattern of a river or fluvial channel supplying the allochthonous material to the shore); this sedimentary material would then be shaped by coastal processes into the basic coastal types to form the framework for mangrove habitats. Many of the coast types of Thom (1982) can be recognised in the study area of this paper, but in detail the coast of tropical Western Australia has been subdivided differently here because diverse processes have operated and consequently more varied regional-scale mangrove systems have formed. For instance, some of the large bays in northwestern Australia have not formed by marine inundation of bedrock, but by inundation of a dune hinterland; some of the sediments are allochthonous, but have been derived from a local dune field; some areas are comprised of autochthonous sediments (*viz.*, the carbonate suite); some coastal landforms are inherited from the Pleistocene (*viz.*, the Pleistocene limestone barriers); in some cases of beach/dune coasts, the setting is not related directly to a fluvial source, but represents the down-drift accumulation of coastal sand, or represents the reworking of older deposits; marine inundation in some areas has developed not only drowned bedrock valleys (rias) but also archipelagos, and locally, just isolated bedrock islands. Also the islands of the Northwest Shelf, formed as residual Pleistocene aeolian units, or as faulted outliers, or as emergent, shoaled Holocene deposits are not readily classified in the scheme of Thom (1982).

In contrast, this study places emphasis on the variety of regional-scale landforms, such as active deltas (and whether they were wave- or tide-dominated), inactive (destroyed) deltas, Pleistocene barrier islands, pre-Holocene, and perhaps even pre-Quaternary ancestral landforms, embayments, various types of islands, amongst others. As described above, the main regional-scale systems that form settings for mangroves in Western Australia are wave-dominated deltas, tide-dominated deltas, barrier island systems, embayments, ria shore and archipelago systems, dune coasts, lagoon systems of various origins, and island complexes.

Semeniuk (1986b) identified four main types of coast for mangrove habitats at the regional scale: ria shores and archipelagos; deltas and barrier islands; sheltered bay/embayments; and gulfs; and showed their distribution along the coast of tropical Western Australia. The present study shows that the mangrove systems in Western Australia are more varied and complex than that outlined in that earlier study (*op. cit.*). Exmouth Gulf was also recognised by Semeniuk (1986b) as a distinct mangrove coastal type as part of the "gulf settings" that included King Sound, Cambridge Gulf, and Exmouth Gulf, whereas Exmouth Gulf is not identified here as a coastal system akin to King Sound, but rather as a geographic entity that straddles two separate systems.

Delineating mangrove regions

Mangrove habitats of tropical Western Australia occur in well defined sectors with differing coastal geomorphology and coastal processes, and identifying such sectors is one approach to the delineation of mangrove regions in Western Australia. Identification of the sedimentary province also is important in the definition of mangrove habitats: simple carbonate mud environments, such as along the Canning Coast, where there is no marked high-tidal facies differentiation for instance, provide different habitats to those areas that present a profusion of facies, such as the ria shores along the Kimberley coast. These types of coastal differences should be recognised in separating mangrove systems. On the basis of sediment differences alone, the mangrove systems of tropical Western Australia could be classed into several major regions.

The combination of coastal geomorphology and sedimentary provinces forms the basis of delineating the mangrove systems of this paper, and with this approach seven systems of mangrove environments have been identified. However, this approach does not involve the biogeography of mangroves, and so some system of combining biogeography and physical factors is required if the natural mangroves regions are to be recognised.

Biogeographically, mangrove regions have been delineated to date either on a combination of biological and climatic criteria (Semeniuk *et al.* 1978), or on biological criteria alone (Bridgewater 1982, 1985). Semeniuk *et al.* (1978) related the mangrove systems and species richness in Western Australia to climate, using the climate boundaries of Thornthwaite (1933; cited in Gentilli 1972). Within the tropical zone were three biogeographic regions: humid to subhumid (Biogeographic Region I) with 15 mangrove species; semiarid (Biogeographic Region II) with 12 species; and arid (Biogeographic Region III) with six species.

Bridgewater (1982, 1985) applied mathematical methods to delineate mangrove regions in Western Australia on species occurrence and abundance, and obtained different biogeographic boundaries to Semeniuk *et al.* (1978).

Combining the geomorphic-sedimentary sectors (which determine whether habitats for particular species will be developed) with climate (which determines species richness) probably provides the best method to define mangrove regions (as distinct from biogeographic regions) in Western Australia. Thus mangrove regions are delineated on the availability of appropriate habitats and species richness. This approach is useful in Western Australia, especially since it is apparent that some sectors described above are restricted to specific climates. For example, ria shores with their variety of habitats at small and medium scales, and their range of geomorphic/stratigraphic mechanisms that facilitate fresh water discharge, are located in the more humid parts of Western Australia. Limestone barrier islands, with less abundant systems for discharging fresh water, fortuitously occur in arid parts of Western Australia, where fresh water is scarce anyway.

The delineation of geomorphic-sedimentary regions is relatively simple, since the various coastal systems appear to have sharp boundaries. The delineation of climate regions, however, is not so simple. As discussed by Gentilli (1972), climate can be classified using different emphases, and climate maps can be constructed for different purposes.

Within mangrove regions, where climate influences the salinity of soils and the physiology and structure of the vegetation, the important climatic parameters would appear to be rainfall, evaporation, temperature, and wind. However, although wind is important in the sedimentological development of habitats for evaporation on tidal flats and in the physiologic stress it places on plants, it is with difficulty that it can be incorporated into integrated climate maps, and two of its more important effects, *viz.*, inducing evaporation to develop saline soils, and inducing transpiration within vegetation, are incorporated in the parameter of evaporation. Climatic regions delineated by integrating the parameters of rainfall, evaporation and temperature thus would appear to be the most useful in analysing and comparing the different mangrove regions.

Choosing a climate map to link with mangrove studies, however, remains a problem. To date there has not been a map generated that adequately integrates the parameters of rainfall, temperature and evaporation suitable for mangrove studies. The most useful maps are those of Thornthwaite (1933, cited in Gentilli 1972), showing climatic regions; Koppen (1936), also showing climatic regions; Gentilli (1972), showing moisture regions as determined by rainfall and temperature; and McBoyle (1973), showing climatic regions as determined by factor analysis of some 20 climate parameters. While in principle the best approach to categorising climate is that of McBoyle (1973), who carried out factor analysis of a range of climatic parameters to give rational boundaries to climate regions on criteria other than vegetation and soils, the results of McBoyle (1973) are not directly useful to mangrove studies in Western Australia. Firstly, only six climate stations are used in the analysis for the whole of the northwestern coastal region; secondly, because evaporation is not used in the analysis; thirdly,

many of the 20 parameters are not directly related to mangrove systems. The systems of Thornthwaite (1933, cited in Gentilli 1972) and Koppen (1936) essentially show the same location of humid, semi-arid and arid regions along the coast. The humid area is sited on the region of the Mitchell Plateau in the Kimberley region; the semi-arid area is sited on the region of Dampier Peninsula-Roebuck Bay, King Sound, Cambridge Gulf, and northeast and southeast extremities of the Kimberley Coast; the arid area is sited on the region of the middle to southern part of the Canning Coast, and all the coast from there to Shark Bay. The system of Gentilli (1972) is essentially similar to Thornthwaite (1933) and Koppen (1936) for coastal regions, but Cambridge Gulf is not classed as the same climate as King Sound.

For purposes of this paper, following the boundaries of Thornthwaite (1933, cited in Gentilli 1972) and Koppen (1936), the three climate regions are: humid/subhumid in the central Kimberley Coast (centred on the Mitchell Plateau area); semi-arid in the areas of Cambridge Gulf, King Sound, northeast and southeast extremities of the Kimberley Coast, the Dampier Peninsula-Roebuck Bay, and the Canning Coast to as far south as Cape Bossut; and arid in the area between Cape Bossut to Shark Bay, encompassing the southern part of the Canning Coast, and all of the Pilbara Coast, the Rowley Shelf Province and the Carnarvon Province.

This method of combining the coastal sectors with climate provides nine major mangrove regions in Western Australia:

1. Cambridge Gulf — semiarid zone.
2. Kimberley Coas — humid/subhumid zone;
3. Kimberley Coast — semiarid zone;
4. King Sound — semiarid zone;
5. Canning Coast — semiarid zone;
6. Canning Coast — arid zone;
7. Pilbara Coast — arid zone;
8. Rowley Shelf Province — arid zone;
9. Carnarvon Province — arid zone.

Most of the regions correspond to the geomorphic-sedimentary sectors, but some sectors encompass two types of climate setting: the Kimberley Coast has two climate types, and the Canning Coast has two climate types. As such, this pattern provides some insight into the regional controls in the elimination of some species of mangroves to southwards within these sectors, because while the climate is changing, the habitat types are similar from one end of the sector to the other. For example, consider the areas of Cape Bossut and Cape Keraudren: the coastal systems and mangrove habitats at both these areas are similar—they are part of the Canning Coast sector with similar arrangement of a limestone barrier protecting an embayment, and both have carbonate mud in the mangrove zone, but Cape Bossut is in the semi-arid part of the Canning Coast, and Cape Keraudren is in the arid part. Cape Bossut has the following common mangrove species: *A. amulata*, *A. corniculatum*, *A. marina*, *B. exaristata*, *C. schultzei*, *C. tagal*, *R. stylosa* and *S. alba*. Cape Keraudren has the following mangrove species: *A. amulata*, *A. corniculatum*, *A. marina*, *B. exaristata*, *C. tagal*, *R. stylosa* and *O. ctodonta*, with the species representative of more northerly areas, *viz.*, *C. schultzei* and *S. alba*, absent.

Global significance of mangrove systems in Western Australia

In general, to assess the significance of mangroves globally it is necessary to determine the species richness of various regions, and the variability of coastal style (habitat setting) where mangroves are located. In order to assess the global significance of mangrove formations specifically in Western Australia, the discussion that follows centres on several inter-related aspects of their subcontinental to regional features: species pool, habitats, climate setting and processes (and specifically in this case the arid zone setting and processes), and inter-relationship of mangrove systems across the climate cline and the geological/geomorphic provinces.

The mangroves of northwestern Australia belong to the Eastern Group (=Old World) of mangroves, centred on the Indian-Pacific Ocean area (Tomlinson 1986), and within this region, they more specifically belong to the Indo-Malesian Group that encompasses Pakistan, India, Burma, Malaysia, Indonesia, Celebes, northern Australia and Papua-New Guinea (Chapman 1977). This Indo-Malesian group is the most species-rich region of mangrove worldwide (Chapman 1976). Within this grouping, however, northern Australia is part of the Northern Australian-Papuan sub-group, being less species-rich than some of the other sub-groups but having some species features unique to that region (Chapman 1977).

In terms of endemism and restricted species, Western Australia does not support any unusual, endemic, or restricted mangrove species. In fact, all mangrove species within Western Australia are common and widespread elsewhere either in northern Australia, or in the Indo-Pacific region proximal to northern Australia, and so in this sense, the mangroves of Western Australia are not globally significant. However, what Western Australia does provide that is of global significance is its richness and variability of habitats for mangroves, from large to small scale, as within the same subcontinent there are major variations in style of coast, oceanographic setting, and climate, that interplay with the regional mangrove species pool. This results in a representative record of variation in species, assemblages, structures and physiognomy which provides excellent case studies of biological response to the physico-chemical environment, and valuable information on their biogeographic patterns.

Locations elsewhere in the world may contain the same type of habitats as in Western Australia, but these tend to be scattered. For instance, mangrove formations are well developed in the deltas of the Niger river and the Ganges river, and in the ria coastal settings of the Malaysian region; but Western Australia presents a wider range of habitats for mangroves at the large to small scale in a relatively shorter tract of coast because the geologically and geomorphically diverse coastline traverses several climatic and oceanographic regions. Here, as described in this paper, the variable coasts, that range from tide-dominated rias to wave-dominated deltas and barriers, span a climate gradient from humid to arid. Where there are extensive tracts of mangrove elsewhere, the habitats are either relatively uniform by comparison to Western Australia, or relatively species-poor. Chapman (1977), for instance, provides a map of the global distribution of mangroves from which it is apparent that the tracts of

coast that are of similar or greater length than that of the northwestern part of Australia are in relatively species-poor regions of the globe, e.g., the west and east coast of Africa and the Gulf of Mexico. However, in contrast, species-rich areas, such as those situated in the Malaysian archipelago, exhibit less coastal variation in their mangrove habitats than those of Western Australia. There are two reasons for this. Firstly, the Malaysian archipelago is island-dominated and centred on the equator, and the climate is ubiquitously tropical humid with little scope for the development of arid-style hinterland or arid-zone-influenced coastal landforms (Trewartha 1968). Secondly, many of the island landforms are high relief because the area is an island arc complex, located on a collision zone between two tectonic plates (Forsyth & Uyeda 1975), and volcanism, tectonism and uplift are prevalent (Uyeda 1978)—consequently many of the coastal landforms are of the ria/archipelago or gulf type.

One of the most species-rich areas for mangroves is in India, but this subcontinent does not present a continuous stretch of mangrove coast within which the various regional gradients could be viewed as well as that in northwestern to northern Australia. Also in India there is a large anthropogenic influence resulting in alteration and destruction of mangroves.

Small-scale features within a given coastal system also provide important information on mangroves and their physical setting. In this regard, the arid coastal setting of the Pilbara region is of global significance, compared to other coasts of similar tropical aridity worldwide, such as the Somalia coast, the Persian Gulf, the Red Sea and Arabian Peninsula coast, the Pakistan coast, the Namibian coast and the northwest African coast, Baja California, and the Peruvian-Chilean coastline (Semeniuk 1993). The literature suggests that most of the tropical coasts that are in an equivalent arid setting to the Pilbara are dominantly of the steep or cliffed rocky shore type, where headlands separate bays and sandy coastal stretches, or are of the aeolian type, or are low gradient sabhka type. Many of those arid coasts that resemble the Pilbara, in their setting and their configuration of alluvial, deltaic and aeolian facies within a coastal plain formed down-slope from a high-relief upland, in fact are tectonic. In the Pilbara, the Quaternary coastal development has not been significantly uplifted, if at all. Hence the complication of tectonics has not disrupted the geomorphic pattern, and the various ensembles of Quaternary sediments are still inter-related in time and space. With subsidence and burial, those sediments that have accumulated in the coastal zone will form a distinct assemblage of stratigraphic units, inter-related synoptically and across unconformities, thus providing a physical framework of coastal types and stratigraphic/hydrologic styles where mangrove habitats can develop. This would suggest that the style of sedimentation and stratigraphic evolution of the Pilbara coastal system is indeed a globally different and useful model of coastal form in an arid setting. It is this very same coastal system that hosts mangroves and also forms the arid zone end of a biogeographic continuum traceable from the more humid areas in the north.

Mangroves of northwestern Australia should be viewed as a continuation of the northern Australian system which incorporates the area from Cambridge Gulf to Darwin, and as part of the climatic cline extending from there into the

Papuan region. There are two significant aspects to this. Firstly, in this context, the variety of large-scale coastal habitat settings of the Western Australian coast can be viewed as significant in that it contrasts with other styles of coasts developed further north in Australia and in the Papuan to Malaysian archipelago settings, which have a predominance of steep shores, high-tidal deltas and ria coastal types (Coleman *et al.* 1970; Bird & Schwartz 1985). This allows researchers to trace the changes in mangrove formations from humid macrotidal zones into arid and microtidal regions, albeit against a changing coastal style, and also from one coastal style (and its smaller scale habitats) to another within the same climatic setting (*e.g.*, ria setting *vs.* barrier island setting *vs.* deltaic setting) in order to compare the differing effects of habitats and climate on mangrove systems. Secondly, the Malesian-Papuan-Northern Australian mangroves form a group that extends far into the higher latitudes. Within this group, the Western Australian coast, being the most arid coast in Australia, uniquely carries the cline of mangrove changes from humid, to semi-arid to arid within a system that globally is the most species-rich mangrove region. In contrast, other coasts in equivalent latitudes, *e.g.*, Southern Africa and South America, are situated in relatively species-poor regions.

The tropical coast of northwestern Australia thus provides an important scientific resource for present and future researchers, and a model for mangrove biogeography and ecology that is useful globally in that it combines within the one coastal tract many aspects of regional scale features found scattered in other parts of the world. In this regard, I consider it to be an excellent and valuable natural laboratory of international significance.

References

- Beard J S 1967 An inland occurrence of mangroves. *The Western Australian Naturalist* 10:112-115.
- Beard J S 1975 The vegetation of the Pilbara area. Explanatory notes to Map Sheet 5 of Vegetation Survey of WA: Pilbara. University of Western Australia Press, Nedlands.
- Bird E C F & Schwartz M L 1985 The world's coastline. Van Nostrand Reinhold, New York.
- Bridgewater P B 1982 Mangrove vegetation of the southern and western Australian coastline. In: *Mangrove ecosystems in Australia: structure, function and management* (ed B F Clough) AIMS & ANU Press, Canberra, 111-120.
- Bridgewater P B 1985 Variation in the mangal along the west coastline of Australia. *Proceedings of the Ecological Society of Australia* 13:243-256.
- Brown R G 1976 Exmouth Gulf. In: *Carbonate sediments of the West Coast of Western Australia* (eds B W Logan, R G Brown & P G Quilty) 25th International Geological Congress, Sydney, 55-75.
- Brown R G 1988 Holocene sediments and environments, Exmouth Gulf, Western Australia. In: *The North West Shelf* (eds P G & R R Purcell) Proc. Petroleum Exploration Society Australia Symposium, Perth, 85-93.
- Bunt J S & Williams W T 1980 Studies in the analysis of data from Australian tidal forests ("mangroves"). I. Vegetational sequences and their graphic representation. *Australian Journal of Ecology* 5:385-390.
- Bureau of Meteorology 1973 The Climate and Meteorology of West. Australia. In: *Western Australian Year Book* 12, Melbourne, 25-59.
- Bureau of Meteorology 1975 Climatic averages Western Australia. Australian Government Publishing Service, Canberra.
- Calder M 1979 Australian National Tide Tables 1980 Australian Hydrographic Publication 11. Australian Government Publishing Service, Canberra.
- Carrigy M A & Fairbridge R W 1954 Recent sedimentation, physiography and structure of the continental shelves of Western Australia. *Journal of the Royal Society of Western Australia* 38:65-95.
- Chapman V J 1976 Mangrove Vegetation. Cramer, Lehre.
- Chapman V J 1977 Introduction. In: *Ecosystems of the World. 1. Wet Coastal Ecosystems* (ed V J Chapman) Elsevier, Amsterdam, 1-29.
- Coleman F 1971 Frequencies, tracks and intensities of tropical cyclones in the Australian region, Nov. 1909-June 1969. Bureau of Meteorology, Australian Government Publishing Service, Canberra.
- Coleman J M, Gagliano S M & Smith W G 1970 Sedimentation in a Malaysian high tide tropical delta. *Society of Economic Palaeontologists and Mineralogists Special Publication* 15:185-197.
- Davie J D S 1985 The mangrove vegetation of the South Alligator River, Northern Australia. In: *Coasts and tidal wetlands of the Australian monsoon region* (eds K N Bardsley, J D S Davie & C D Woodroffe) NARU, Australian National University, Mangrove Monograph No. 1, 133-151.
- Davies G R 1970 Carbonate bank sedimentation eastern Shark Bay, Western Australia. In: *Carbonate sedimentation and environments, Shark Bay, Western Australia*. American Association of Petroleum Petrologists Memoir 13, 85-168.
- Davies J L 1977 The coast. In: *Australia, a geography* (ed D N Jeans) Sydney University Press, Sydney, 134-151.
- Easton A K 1970 The tides of the continent of Australia. Horace Lamb Centre Oceanographic Research, Flinders University, South Australia, Research Paper No. 37.
- Forsyth D & Uyeda S 1975 On the relative importance of the driving forces of plate motion. *Geophysical Journal* 43:163-200.
- Galloway R W 1982 Distribution and physiographic patterns of Australian mangroves. In: *Mangrove ecosystems in Australia: structure, function and management* (ed B F Clough) AIMS & ANU Press, Canberra, 31-54.
- Gentili J 1971 Climates of Australia and New Zealand. *World Survey of Climatology* 13, Elsevier, Amsterdam.
- Gentili J 1972 Australian Climate Patterns. Nelson, Melbourne.
- Geological Survey of Western Australia 1975 The geology of Western Australia. Geological Survey of Western Australia Memoir 2, Perth.
- Gill E D 1982 Eight coasts of Australia. CSIRO Division of Applied Geomechanics, Technical Report 119, Mt. Waverley, Vic.
- Jennings J 1975 Desert dunes and estuarine fill in the Fitzroy estuary, northwestern Australia. *Catena* 2:215-262.
- Jennings J & Bird E C 1967 Regional geomorphological characteristics of some Australian estuaries. In: *Estuaries* (ed G H Lauff) American Association for the Advancement of Science, Washington D.C., 121-128.
- Johnson D P 1982 Sedimentary facies of an arid zone delta: Gascoyne delta, Western Australia. *Journal of Sedimentary Petrology* 52:547-563.
- Jutson J T 1950 The physiography (geomorphology) of Western Australia. Western Australian Geological Survey Bulletin 95, Perth.
- Koppen W 1936 Das Geographische System der Klimate. Vol 1C, In: *Handbuch der Klimatologie* (W Koppen & R Geiger). Berlin.
- Logan B W 1987 The MacLeod evaporite basin, Western Australia. American Association of Petroleum Geologists Memoir 44, Tulsa, Oklahoma.
- Logan B W, Read J F, & Davies G R 1970 History of carbonate sedimentation, Quaternary Epoch, Shark Bay, Western Australia. In: *Carbonate sedimentation and environments, Shark Bay, Western Australia*. American Association of Petroleum Geologists Memoir 13, p. 38-83, Tulsa, Oklahoma.
- Lourensz R S 1981 Tropical cyclones in the Australian region, July 1909 to June 1980. Bureau of Meteorology, Australian Government Publishing Service, Canberra.
- Lugo A E & Snedaker S C 1976 The ecology of mangroves. *Annual Reviews of Ecology & Systematics* 5:39-64.
- MacNae W 1968 A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. *Advances in Marine Biology* 6:73-270.
- McBoyle G R 1973 Climatic classification of Australia by computer. *Australian Geographical Studies* IX:1-14.
- Milton D 1978 The rainfall from tropical cyclones in West Australia. Geowest. Working Papers, Department of Geography, University of Western Australia 13, 61p.
- Saenger P, Specht M M, Specht R L & Chapman V J 1977 Mangal and coastal salt marsh communities in Australasia. In: *Ecosystems of the World. 1. Wet Coastal Ecosystems* (ed V J Chapman) Elsevier, Amsterdam, 293-345.
- Semeniuk V 1980a Mangrove zonation along an eroding coastline in King Sound, North-Western Australia. *Journal of Ecology* 68:789-812.
- Semeniuk V 1980b Quaternary stratigraphy of the tidal flats King Sound, Western Australia. *Journal of the Royal Society of Western Australia* 63:65-78.

- Semeniuk V 1981a Long-term erosion of the tidal flats King Sound, North-Western Australia. *Marine Geology* 43:21-48
- Semeniuk V 1981b Sedimentology and the stratigraphic sequence of a tropical tidal flat, North-Western Australia. *Sedimentary Geology*, 29:195-221
- Semeniuk V 1982 Geomorphology and Holocene history of the tidal flats, King Sound, North Western Australia. *Journal of the Royal Society of Western Australia* 65:47-68.
- Semeniuk V 1983 Regional and local mangrove distribution in Northwestern Australia in relationship to freshwater seepage. *Vegetatio* 53:11-31.
- Semeniuk V 1985 Development of mangrove habitats along ria coasts in north and northwestern Australia. *Vegetatio* 60:3-23.
- Semeniuk V 1986a Terminology for geomorphic units and habitats along the tropical coast of Western Australia. *Journal of the Royal Society of Western Australia* 68:53-79.
- Semeniuk V 1986b Threats to, and exploitation and destruction of, mangrove systems in Western Australia In: *Mangrove Ecosystems of Asia and the Pacific; status, exploitation and management* (eds C D Field & A J Dartnall) Proceedings Research for Development Seminar, Australian Institute of Marine Science, Townsville, 228-240.
- Semeniuk V 1993 The Pilbara coast: a riverine coastal plain in a tropical arid setting, Northwestern Australia In: *Late Quaternary evolution of coastal and lowland riverine plains of southeast Asia and northern Australia* (ed C D Woodroffe) *Sedimentary Geology* 83:235-256
- Semeniuk V & Wurm P A S 1987 Mangroves of the Dampier Archipelago, Western Australia. *Journal of the Royal Society of Western Australia* 69:29-87.
- Semeniuk V, Chalmer P N & LeProvost I 1982 The marine environments of the Dampier Archipelago: *Journal of the Royal Society of Western Australia* 65:97-114.
- Semeniuk V, Kenneally K F & Wilson P G 1978 Mangroves of Western Australia. Handbook 12, Western Australian Naturalists Club, Perth.
- Specht R L 1981 Foliage protective cover and standing biomass. In: *Vegetation classification in Australia* (eds A N Gillison & D J Anderson) CSIRO & ANU Press, Canberra.
- Steedman R K 1985 Air quality meteorology of the Burrup Peninsula, Western Australia, June 1982 to December 1984. Vol.1 text and appendices A to G. RK Steedman Ltd. Report No. R271 Aug 1985. Unpublished Report to Woodside Offshore Petroleum Ltd.
- Steedman R K & Colman E J 1985 On the joint probability of extreme winds, waves and currents at North Rankin 'A', north western Australia. In: *The application of joint probability of Metocean phenomena in the oil industry's structural design work*. The Oil Industry International Exploration & Production Forum, London, Paper 1, 20p.
- Thom B G 1967 Mangrove ecology and deltaic geomorphology: Tabasco, Mexico. *Journal of Ecology* 55:301-343.
- Thom B G 1982 Mangrove ecology—a geomorphic perspective. In: *Mangrove ecosystems in Australia: structure, function and management* (ed B F Clough) AIMS & ANU Press, Canberra, 301-343.
- Thom B G, Wright L D & Coleman J M 1975 Mangrove ecology and deltaic-estuarine geomorphology. *Journal of Ecology* 63:203-232.
- Tomlinson P B 1986 The botany of mangroves. Cambridge University Press, Cambridge.
- Trewartha G T 1968 An introduction to climate. McGraw-Hill, New York.
- Uyeda S 1978 The new view of the earth. W H Freeman & Co., San Francisco.
- Wells A G 1981 A survey of riverside mangrove vegetation fringing tidal river systems of Kimberley, Western Australia. In: *Biological Survey of Mitchell Plateau and Admiralty Gulf, Western Australia*. Western Australian Museum Supplement No 3, 95-121.
- Wells A G 1982 Mangrove vegetation of northern Australia. In: *Mangrove ecosystems in Australia: structure, function and management* (ed B F Clough) AIMS & ANU Press, Canberra 57-78.
- Woods P G 1980 Coastal management in Western Australia. Department of Conservation & Environment Bulletin 49, Perth.
- Woods P G, Webb M J & Eliot I G 1985 Western Australia In: *The World's Coastline* (eds E C F Bird & M L Schwartz) Van Nostrand Reinhold, New York, 929-947.

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Notes. — The numbers in brackets after each entry are the year of election to membership and, where appropriate, to Honorary or Life membership. In the list of members, a superscript indicates Associate Member (^a), Institutional Member (ⁱ), Life Member (^l) or Student Member (^s).

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Members

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 Allen, A. D. Geological Survey of WA, EAST PERTH. WA 6004 (1976).
 Allender, J. F. UNLEY. SA 5061 (1974).
 Arbuckle, D. J. F. FARRAMERE. Republic of South Africa (1983).
 Armstrong, C. J. ARMADALE. WA 6112 (1991).
 Atkins, R. P. Waterways Commission, PERTH. WA 6000 (1976).
 Atkinson, D. M. M. CLAREMONT. WA 6010 (1976).
 Atkinson, P. R. AUCKLAND NEW ZEALAND (1970).
 Backhouse, J. Geological Survey of WA, EAST PERTH. WA 6004 (1976).
 Bailey, J. M. Environmental & Life Sciences, Murdoch University, MURDOCH. WA 6150 (1988).
 Baker, S. K. School of Agriculture, University of Western Australia, NEDLANDS. WA 6009 (1987).
 Balla, S. A. HILTON. WA 6163 (1992).
 Balme, B. E. CLAREMONT. WA 6010 (1958).
 Balme, J. M. Department of Archaeology, University of New England, ARMIDALE. NSW 2351 (1976).
 Bamford, A. R. KINGSLEY. WA 6026 (1988, 1988)^a.
 Bamford, M. J. KINGSLEY. WA 6026 (1988).
 Bannister, J. L. WA Museum, Francis Street, PERTH. WA 6000 (1967).
 Barley, M. E. Geology Department, University of Western Australia, NEDLANDS. WA 6009 (1987).
 Bayly, I. A. E. Department of Ecology & Evolutionary Biology, Monash University, CLAYTON. VIC 3168 (1992).
 Baynes, A. WA Museum, PERTH. WA 6000 (1967).
 Beere, G. M. MEEKATHARRA. WA 6642 (1980).
 Beggs, B. J. BOORAGOON. WA 6154 (1971).
 Bekle, H. DIANELLA. WA 6062 (1982).
 Bell, D. T. Botany Department, University of Western Australia, NEDLANDS. WA 6009 (1977).
 Bennett, E. M. GOOSEBERRY HILL. WA 6076 (1963).
 Berry, P. F. WA Museum, PERTH. WA 6000 (1980).
 Birch, P. V. Perth Observatory, BICKLEY. WA 6076 (1987).
 Black, W. R. Zoology Department, University of Western Australia, NEDLANDS. WA 6009 (1987).
 Blyth, J. D. Dept Conservation & Land Management, CRAWLEY. WA 6009 (1987).
 Boardman, W. J. SALTER POINT. WA 6152 (1984).
 Borowitzka, M. A. Biological & Environmental Sciences, Murdoch University, MURDOCH. WA 6150 (1986).
 Bottomley, G. A. CLAREMONT. WA 6010 (1971).
 Bougher, A. R. MOUNT HAWTHORN. WA 6016 (1987).
 Bourgault du Coudray, P. L. WEST MIDLAND. WA 6056 (1991)^s.
 Bowdler, S. Dept of Archaeology, University of Western Australia, NEDLANDS. WA 6009 (1983).
 Bowen, B. K. NEDLANDS. WA 6009 (1958)^a.
 Bowers, C. L. KALAMUNDA. WA 6076 (1987).

Bradley, J. S. Environmental Sciences, Murdoch University, MURDOCH. WA 6150. (1993)
 Brearly, A. Dept Botany, University of Western Australia, NEDLANDS. WA 6009. (1993)^s.
 Bradshaw, S. D. Zoology Department, University of Western Australia, NEDLANDS. WA 6009 (1965).
 Bridge, P. J. VICTORIA PARK. WA 6100 (1966).
 Bridgewater, P. Australian National, Parks and Wildlife Service, CANBERRA. ACT 2601 (1976).
 Briggs, I. M. NEDLANDS. WA 6009 (1983).
 Brooker, M. G. CSIRO, Division of Wildlife Research, MIDLAND. WA 6056 (1987).
 Brown, R. G. Geology Department, University of Western Australia, NEDLANDS. WA 6009 (1987).
 Buirchell, B. J. EAST VICTORIA PARK. WA 6101 (1991).
 Bunn, E. R. Kings Park & Botanical Gardens, WEST PERTH. WA 6005 (1985).
 Bunn, S. E. School Aust. Environ. Studies, Griffith University, NATHAN. QLD 4111 (1985).
 Burbidge, A. A. WA Wildlife Research Centre, Dept Conservation & Land Management, WANNEROO. WA 6065 (1983).
 Burbidge, A. H. WA Wildlife Research Centre, Dept Conservation & Land Management, WANNEROO. WA 6065 (1978).
 Burman, R. R. Physics Department, University of Western Australia, NEDLANDS. WA 6009 (1988).
 Burne, R. V. Bureau of Mineral Resources, CANBERRA. ACT 2601 (1991).
 Butler, R. J. T. SOUTH GUILDFORD. WA 6055 (1965).
 Calver, M. C. ALFRED COVE. WA 6154 (1989).
 Candy, M. P. Perth Observatory, BICKLEY. WA 6076 (1985).
 Cannon, J. R. Dept Organic Chemistry, University of Western Australia, NEDLANDS. WA 6009 (1987).
 Carey, S. W. DYNMYRNE. TAS 7005 (1933, 1933)^l.
 Chalmer, P. N. TINGLEDAL. WA 6333 (1981).
 Chambers, F. M. ROCKINGHAM. WA 6168 (1992).
 Chiffings, A. W. NEWTOWN. VIC 3220 (1980).
 Christensen, P. E. S. BALINGUP. WA 6253 (1978).
 Churchill, D. M. APOLLO BAY. VIC 3233 (1956).
 Cock, D. J. MOUNT CLAREMONT. WA 6010 (1987)^a.
 Cockbain, A. E. SOUTH PERTH. WA 6151 (1976).
 Coleman, P. J. Geology Department, University of Western Australia, NEDLANDS. WA 6009 (1963).
 Collins, M. T. MELVILLE. WA 6156 (1990).
 Collins, P. WOODLANDS. WA 6018 (1987).
 Colquhoun, I. J. Alcoa of Australia, APPLECROSS. WA 6153 (1983).
 Colreavy, M. P. NORTH PERTH. WA 6006 (1988)^a.
 Conacher, A. J. Geography Department, University of Western Australia, NEDLANDS. WA 6009 (1972).
 Congdon, R. A. Botany Department, James Cook University, TOWNSVILLE. QLD 4811 (1975).
 Connell, S. W. Weed Science Branch, Department of Agriculture, SOUTH PERTH. WA 6151 (1988).
 Considine, J. A. School of Agricultural Science, University of Western Australia, NEDLANDS. WA 6009 (1987).

- Cowling, W. A. SOUTH PERTH. WA 6151 (1983).
- Crawford, I. M. FLOREAT. WA 6014 (1961).
- Creed, K. E. School of Veterinary Studies, Murdoch University, MURDOCH. WA 6150 (1987).
- Cresswell, I. D. BELCONNEN. ACT 2616 (1987).
- Crombie, D. S. Dept Conservation & Land Management DWELLINGUP. WA 6213 (1985).
- Crossland, P. A. LESMURDIE. WA 6076 (1981)^A.
- Curnow, D. H. MOSMAN PARK. WA 6012 (1956)^A.
- Davies, S. J. J. MOUNT HELENA. WA 6555 (1977).
- Davis, C. E. S. FLOREAT PARK. WA 6014 (1938).
- Davison, E. M. Dept Conservation & Land Management, COMO. WA 6152 (1982).
- Davy, R. Geological Survey of WA, EAST PERTH. WA 6004 (1966).
- De Laeter, J. R. WILLETON. WA 6155 (1972).
- del Marco, A. P. NORTH PERTH. WA 6006 (1992).
- Dell, B. Biological & Environmental Sciences, Murdoch University, MURDOCH. WA 6150 (1975).
- Dickman, C. R. School of Biological Sciences, University of Sydney, SYDNEY. NSW 2006 (1986).
- Dixon, K. W. CITY BEACH. WA 6015 (1984).
- Dodd, J. Department of Agriculture, SOUTH PERTH. WA 6151 (1978).
- Dodds, F. S. WEMBLEY. WA 6014 (1972).
- Doupe, R. G. WEST PERTH. WA 6005 (1992).
- Dring, R. S. BOORAGOON. WA 6154 (1975).
- Dyson, S. E. MOUNT PLEASANT. WA 6153 (1993).
- Eastman, W. H. AUSTRALIND. WA 6230 (1963).
- Edinger-Reeve, R. BAYSWATER. WA 6053 (1988).
- Eliot, I. G. Geography Department, University of Western Australia, NEDLANDS. WA 6009 (1981).
- Elkington, C. R. KENWICK. WA 6107 (1958).
- Elliott, R. M. L. ROLEYSTONE. WA 6111 (1987)^A.
- Evans, C. A. FLOREAT. WA 6014 (1990).
- Farrington, P. KARRINYUP. WA 6018 (1981).
- Ferguson, W. C. ST KILDA. VIC 3182 (1978).
- Field, R. A. JANDAKOT. WA 6164 (1984).
- Firman, J. B. NORTH LAKE. WA 6163 (1988).
- Foulds, W. GNANGARA. WA 6065 (1981).
- Fox, J. E. D. School of Biology, Curtin University of Technology, BENTLEY. WA 6102 (1975, 1976)^A.
- Friend, G. R. WA Wildlife Research Centre, Dept Conservation & Land Management, WANNEROO. WA 6065 (1987).
- Friend, J. A. WA Wildlife Research Centre, Dept Conservation & Land Management, WANNEROO. WA 6065 (1987).
- Froend, R. H. BICTON. WA 6157 (1988).
- Gardner, P. E. NORTH FREMANTLE. WA 6159 (1992).
- Gazey, P. MAIDA VALE. WA 6057 (1993)^A.
- Geary, J. K. KARRINYUP. WA 6018 (1943).
- George, A. S. GORDON. ACT 2906 (1961).
- George, P. R. KARRINYUP. WA 6018 (1987).
- Ghisalberti, E. L. NEDLANDS. WA 6009 (1989).
- Gibson, N. WA Wildlife Research Centre, Dept Conservation & Land Management, WANNEROO. WA 6065 (1991).
- Gladstones, J. S. CITY BEACH. WA 6015 (1957).
- Glassford, D. K. BULLCREEK. WA 6149 (1984).
- Goble-Garratt, E. M. WEST LEEDERVILLE. WA 6007 (1989).
- Gole, M. J. GOOSEBERRY HILL. WA 6076 (1984).
- Gordon, D. M. LeProvost Environmental Consultants, COMO. WA 6152 (1979).
- Gozzard, J. R. Geological Survey of WA, EAST PERTH. WA 6004 (1989).
- Graham, J. CSIRO, Division of Mineralogy, WEMBLEY. WA 6014 (1973).
- Gray, N. M. HUNTERS HILL. NSW 2110 (1948).
- Grayling, P. M. FREMANTLE. WA 6160 (1984).
- Griffin, E. A. VICTORIA PARK. WA 6100 (1978).
- Groves, D. I. Geology Department, University of Western Australia, NEDLANDS. WA 6009 (1971).
- Haig, D. W. Geology Department, University of Western Australia, NEDLANDS. WA 6009 (1985).
- Hall, G. P. COMO. WA 6152 (1990).
- Hall, H. I. E. YORK. WA 6302 (1951).
- Hallam, S. J. YORK. WA 6302 (1967).
- Hallberg, J. A. NEERABUP. WA 6031 (1970).
- Halse, S. A. WA Wildlife Research Centre, Dept Conservation & Land Management, WANNEROO. WA 6065 (1992).
- Hamilton, R. KALGOORLIE. WA 6430 (1991).
- Hare, R. SAN LORENZO. MANILA PHILIPPINES (1950).
- Harris, P. G. NEDLANDS. WA 6009 (1976).
- Hart, R. P. SHENTON PARK. WA 6008 (1982).
- Harvey, M. S. WA Museum, PERTH. WA 6000 (1992).
- Hatcher, B. G. Department of Oceanography, Dalhousie University, HALIFAX. NOVA SCOTIA. CANADA (1987).
- Hefter, G. School of Physical and Mathematical Sciences, Murdoch University. MURDOCH. WA 6150 (1993).
- Hesp, P. A. SINGAPORE (1992).
- Hilliard, R. W. GREENMOUNT. WA 6056 (1993).
- Hillman, R. M. DALKEITH. WA 6009 (1987).
- Hilton, R. N. NEDLANDS. WA 6009 (1966)^A.
- Hnatiuk, R. J. COOK. ACT 2614 (1976).
- Hobbs, A. A. Department of Biochemistry, University of Western Australia, NEDLANDS. WA 6009 (1992).
- Hobbs, R. J. CSIRO, Division of Wildlife Research, MIDLAND. WA 6056 (1984).
- Hobbs, V. J. Mathematical & Physical Sciences, Murdoch University, MURDOCH. WA 6150 (1984).
- Hobday, J. D. MOSMAN PARK. WA 6012 (1974).
- Hodgson, E. C. DAGLISH. WA 6008 (1946).
- Hopkins, E. R. MANNING. WA 6152 (1959).
- Hopper, S. D. Kings Park & Botanical Gardens, WEST PERTH. WA 6005 (1985).
- Hopwood, J. M. Mathematics Department, University of Western Australia, NEDLANDS. WA 6009 (1989).
- Horwitz, P. H. J. Environmental Management, Edith Cowan University, JOONDALUP. WA 6027 (1987).
- Horwitz, R. C. DARLINGTON. WA 6070 (1963)^A.
- Hos, D. P. C. MOSMAN PARK. WA 6012 (1974).
- Howden, P. R. ATTADALE. WA 6156 (1963).
- Ingram, B. S. DIANELLA. WA 6062 (1966).
- Isted, W. T. C. MOUNT PLEASANT. WA 6153 (1976).
- Jablonski, N. G. Department of Anatomy & Human Biology, University of Western Australia, NEDLANDS. WA 6009 (1991).
- James, S. A. WOODLANDS. WA 6018 (1993)^A.
- Jasinska, E. J. Dept of Zoology, University of Western Australia, NEDLANDS. WA 6009 (1992).
- Johnson, G. I. KALGOORLIE. WA 6430 (1990).
- Johnston, D. B. ATTADALE. WA 6156 (1987).
- Johnstone, M. H. CARLINGFORD. NSW 2118 (1949).
- Jones, F. G. W. APPLECROSS. WA 6153 (1992)^A.
- Jones, M. G. K. APPLECROSS. WA 6153 (1992).
- Jones, R. A. C. Department of Agriculture, SOUTH PERTH. WA 6151 (1992).
- Joske, R. A. CLAREMONT. WA 6010 (1987)^A.
- Keay, J. Kespen Pty Ltd 5 Gloucester Street, SWANBOURNE. WA 6010 (1969).
- Keeley, G. J. PALMYRA. WA 6157 (1984).
- Keighery, G. J. WA Wildlife Research Centre, Dept Conservation & Land Management, WANNEROO. WA 6065 (1976).
- Kendrick, G. W. WA Museum, PERTH. WA 6000 (1965).
- Kenneally, K. F. WA Herbarium, Dept Conservation & Land Management, COMO. WA 6152 (1969).
- Kinncar, A. C. WEMBLEY DOWNS. WA 6019 (1978).
- Kinncar, J. E. WEMBLEY DOWNS. 6019 (1978).
- Klemm, V. V. MANDURAH. WA 6120 (1987).
- Ladd, P. Biological & Environmental Sciences, Murdoch University, MURDOCH. WA 6150 (1987).
- Lamont, B. B. School of Biology, Curtin University of Technology, BENTLEY. WA 6102 (1972).
- Lawrence, M. E. FORRESTFIELD. WA 6058 (1987).
- Lenanton, R. J. Fisheries Department, WA Marine Research Laboratory, NORTH BEACH. WA 6020 (1974).
- Leprovost, M. I. LeProvost Environmental Consultants, COMO. WA 6152 (1987).
- Library Board of WA, Alexander Library Building, Perth Cultural Centre, PERTH. WA 6000.
- Lintern, M. J. MOUNT HAWTHORN. WA 6016 (1987).
- Littlejohn, M. J. Zoology Department, University of Melbourne, PARKVILLE. VIC 3052 (1956).
- Longnecker, N. Soil Science, University of Western Australia, NEDLANDS. WA 6009 (1993).
- Loneragan, J. F. Environmental & Life Sciences, Murdoch University, MURDOCH. WA 6150 (1961).
- Loneragan, N. R. CSIRO Marine Laboratories, CLEVELAND. QLD 4163 (1981).
- Loneragan, O. W. BENTLEY. WA 6102 (1964)^A.
- Loneragan, W. A. Botany Department, University of Western Australia, NEDLANDS. WA 6009 (1963).
- Lord, J. H. NEDLANDS. WA 6009 (1942).
- Lukis, M. F. F. NEDLANDS. WA 6009 (1948)^A.
- Lund, M. A. Environmental Management, Edith Cowan University, JOONDALUP. WA 6027 (1993).

- Luscombe, A F. CARINE. WA 6020 (1990).
- Lynch, D A. Geology Department, University of Western Australia, NEDLANDS. WA 6009 (1990)[†].
- Lyons, T J. Biological & Environmental Sciences, Murdoch University, MURDOCH. WA 6150 (1988).
- Macey, D J. Biological & Environmental Sciences, Murdoch University, MURDOCH. WA 6150 (1990).
- Macfarlane, T D. Manjimup Research Centre, Dept Conservation & Land Management, MANJIMUP. WA 6258 (1973).
- Main, B Y. Zoology Department, University of Western Australia, NEDLANDS. WA 6009 (1952).
- Majer, J D. School of Biology, Curtin University of Technology, Hayman Road, BENTLEY. WA 6102 (1974).
- Manning, C R. APPLECROSS. WA 6153 (1991).
- Marchant, N G. WA Herbarium, Dept Conservation & Land Management, COMO. WA 6152 (1963).
- Marsh, L M. COTTESLOE. WA 6011 (1955).
- Marshall, J K. CSIRO, WEMBLEY. WA 6014 (1974).
- Masters, B K. CAPEL. WA 6271 (1970).
- McArthur, W M. ALFRED COVE. WA 6154 (1951).
- McCaw, W L. Dept Conservation & Land Management, MANJIMUP. WA 6258 (1986).
- McComb, A J. Environmental Science, Murdoch University, MURDOCH. WA 6150 (1963).
- McComb, J A. Biological & Environmental Sciences, Murdoch University, MURDOCH. WA 6150 (1974)[†].
- McGrath, J F. BUSSELTON. WA 6280 (1984).
- McMillan, R P. COTTESLOE. WA 6011 (1956).
- McNamara, K J. WA Museum, PERTH. WA 6000 (1979).
- Mees, G F. BUSSELTON. WA 6280 (1959).
- Merrifield, H E. ROCKINGHAM. WA 6168 (1969).
- Millington, A J. KUNUNURRA. WA 6743 (1952).
- Mills, C H. BASSENDEAN. WA 6054 (1986).
- Milne, V A. ALBANY. WA 6330 (1987).
- Moore, L S. GREENMOUNT. WA 6056 (1990).
- Morgan, K H. K H Morgan and Associates, Consulting Geologists, VICTORIA PARK. WA 6100 (1961).
- Morgan, W R. COMO. WA 6152 (1961).
- Morrison, D A. SCARBOROUGH. WA 6019 (1987).
- Morrison, P F. SOUTH PERTH. WA 6151 (1993).
- Moulds, M S. WAITARA. NSW 2077 (1965)[†].
- Muir, B G. BOYA. WA 6056 (1967).
- Mulcahy, M J. NEDLANDS. WA 6009 (1955)[†].
- Murphy, D P. HELENA VALLEY. WA 6056 (1993).
- Myers, J S. Geological Survey of WA, EAST PERTH. WA 6004 (1987).
- Nash, D W. WEMBLEY. WA 6014 (1972).
- Noel, D. SUBIACO. WA 6008 (1989).
- Nowak, I R. COMO. WA 6152 (1976)[†].
- O'Shea, J E. Department of Zoology, University of Western Australia, NEDLANDS. WA 6009 (1992).
- Oldham, J A. FLOREAT. WA 6014 (1987).
- Orsini, J P. SWANBOURNE. WA 6010 (1992).
- Osborne, J M. Curtin University of Technology, PERTH. WA 6001 (1985).
- Osman, A H. KILLARA. NSW 2071 (1962).
- Oxnard, C. Dept Anatomy and Human Biology, University of Western Australia, NEDLANDS. WA 6009 (1993).
- Parker, C A. NEDLANDS. WA 6009 (1959). Medallist 1986.
- Parker, I N. SOUTH FREMANTLE. WA 6162 (1988).
- Pate, J S. Botany Department, University of Western Australia, NEDLANDS. WA 6009 (1977).
- Pearce, A F. DUNCRAIG. WA 6023 (1981).
- Pearce, R H. KALAMUNDA. WA 6076 (1955).
- Pearman, G I. CSIRO, Div of Atmospheric Research, MORDIALLOC. VIC 3195 (1963).
- Peaty, C E. DAGLISH. WA 6008 (1985)[†].
- Pett, L J. DALKEITH. WA 6009 (1965).
- Perry, D H. VICTORIA PARK. WA 6100 (1959).
- Perry, G. WA Herbarium, Dept Conservation & Land Management, COMO. WA 6152 (1966).
- Perry, M W. Department of Agriculture, SOUTH PERTH. WA 6151 (1971).
- Playford, P E. NEDLANDS. WA 6009 (1952).
- Podger, F. (1993).
- Poole, W E. DICKSON. ACT 2602 (1951).
- Potter, I C. SALTERS POINT. WA 6152 (1981).
- Prendergast, W F. CLAREMONT. WA 6010 (1985, 1985)[†].
- President of the Australian Institute of Agricultural Science, c/o Department of Agriculture, SOUTH PERTH. WA 6151[†].
- Price, L K. BELMONT. WA 6104 (1987).
- Purcell, P G. SCARBOROUGH. WA 6019 (1989).
- Quilty, P G. Antarctic Division, Channel Highway, KINGSTON. TAS 7150 (1962).
- Ravine, D. CYNCOED. CARDIFF, WALES UNITED KINGDOM (1983).
- Rice, G E. RINGWOOD EAST. VIC 3135 (1980).
- Rich, P J. Department of Education, Hoover Institution, Stanford. California USA. (1991).
- Ride, W D L. HUGHES. ACT 2605 (1958).
- Ridsdill-Smith, T J. CSIRO, Division of Entomology, WEMBLEY. WA 6014 (1980).
- Rimes, G D. WATTLE GROVE. WA 6107 (1956)[†].
- Roberts, F J. NEDLANDS. WA 6009 (1958)[†].
- Roberts, J D. Dept Zoology, University of Western Australia, NEDLANDS. WA 6009 (1993).
- Robinson, S J. SOUTH PERTH. WA 6151 (1985)[†].
- Roe, R. KENSINGTON. WA 6151 (1969).
- Rook, M K. NORTH PERTH. WA 6006 (1986).
- Rooke, I J. MARGARET RIVER. WA 6285 (1982).
- Rowley, I C R. GUILDFORD. WA 6055 (1987)[†].
- Sanders, C C. Environmental Protection Authority, PERTH. WA 6000 (1968).
- Sappal, K K. School of Applied Geology, Curtin University of Technology, PERTH. WA 6001 (1991).
- Saunders, D A. GUILDFORD. WA 6055 (1983).
- Scott, J. School of Applied Geology, Curtin University of Technology, PERTH. WA 6001 (1991).
- Scott, J K. CSIRO Division of Entomology, WEMBLEY. WA 6014 (1978).
- Scott, W D. Atmospheric Sciences, Biological & Environmental Sciences, Murdoch University, MURDOCH. WA 6150 (1991).
- Searle, D J. DALKEITH. WA 6009 (1987).
- Seddon, G. Department of English, University of Western Australia, NEDLANDS. WA 6009 (1962).
- Semeniuk, C A. WARWICK. WA 6024 (1986).
- Semeniuk, V. WARWICK. WA 6024 (1979).
- Shand, COTTESLOE. WA 6011[†].
- Shaw, S E. School of Earth Sciences, Macquarie University, NORTH RYDE. NSW 2109 (1959).
- Shearer, B L. Research Centre, Dept Conservation and Land Management, COMO. WA 6152 (1968).
- Shivas, R G. DOUBLEVIEW. WA 6018 (1988).
- Shugg, H B. APPLECROSS. WA 6153 (1959).
- Smith, V M J. ATTADALE. WA 6156 (1983)[†].
- Smith, E B J. ATTADALE. WA 6156 (1969).
- Smith, L A. WA Museum, PERTH. WA 6000 (1972).
- Sproul, A N. MOUNT PLEASANT. WA 6153 (1978).
- Stace, H. Botany Department, University of Western Australia, NEDLANDS. WA 6009 (1993).
- Start, A N. ROLEYSTONE. WA 6111 (1979).
- Steer, B T. COMO. WA 6152 (1987).
- Stephens, L J. ROLEYSTONE. WA 6111 (1985).
- Stephenson, N C. Department of Geology & Geophysics, University of New England, ARMIDALE. NSW 2350 (1969).
- Stoneman, G. CITY BEACH. WA 6015 (1988).
- Sweetingham, M W. EAST FREMANTLE. WA 6158 (1990).
- Tassell, C B. Queen Victoria Museum & Art Gallery, LAUNCESTON. TAS 7250 (1976).
- Taylor, J C. DALKEITH. WA 6009 (1970).
- Thomas, L N. EAST FREMANTLE. WA 6158 (1987).
- Tingay, A. DARLINGTON. WA 6070 (1991).
- Tippett, J. WALPOLE. WA 6398 (1981)[†].
- Trendall, A F. Geological Survey of WA, EAST PERTH. WA 6004 (1963).
- Triffitt, M A. NEDLANDS. WA 6009 (1987).
- Underwood, R. Institute of Foresters, c/o Dept Conservation & Land Management, COMO. WA 6152[†].
- Utting, E P. MOSMAN PARK. WA 6012 (1963, 1990)[†].
- WA Museum, PERTH. WA 6000[†].
- Walker, D I. Botany Department, University of Western Australia, NEDLANDS. WA 6009 (1989).
- Wallace, G I. The Geraldton Museum, GERALDTON. WA 6530 (1980).
- Wardell-Johnson, G W. BRIDGETOWN. WA 6255 (1987).
- Whitaker, D. KINGSLEY. WA 6026 (1993).
- Wilkinson, D S. MT HAWTHORN. WA 6016 (1992).
- Willmott, S P. FORRESTFIELD. WA 6058 (1962).
- Wills, R T. W A Herbarium, COMO. WA 6152 (1990).
- Withers, P C. Zoology Department, University of Western Australia, NEDLANDS. WA 6009 (1987).
- Woodall, R. CRAFTERS. SA 5152 (1955).
- Woods, P J. COTTESLOE. WA 6011 (1987).
- Wooler, S. ROSSMOYNE. WA 6148 (1990).
- Wooler, R D. Biological Sciences, Murdoch University, MURDOCH. WA 6150 (1993).
- Wurm, P A S. Science Faculty, N.T. University, CASUARINA. NT 0811 (1987).
- Wycheley, P R. SUBIACO. WA 6008 (1972).
- Youngson, W K. WANNEROO. WA 6065 (1987).
- Yu, B. SUNNYBANK. QLD 4109 (1993).

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 di Scienze Naturali, presso Museo Civ. di Storia Naturale. MILANO.
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 Geo Abstracts Ltd. NORWICH. ENGLAND.
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 Geologiques et Minières, Service Geologique National. ORLEANS.
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 Sociedad Científica Argentina. BUENOS AIRES. ARGENTINA.
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 Staatliches Museum für Tierkunde. DRESDEN. GERMANY.
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 Tauschstelle der Naturforsch. BASEL. SWITZERLAND.
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 Tulane Riverside Research Laboratory, BELLE CHASSE. LOUISIANA. USA.
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 Universidade de Aveiro. AVEIRO. PORTUGAL.
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 University of Queensland. ST LUCIA. QLD.
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 University of Washington Library. SEATTLE. WASHINGTON. USA.
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 Waite Agricultural Research Institute. GLEN OSMOND. SA.
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 Western Australian Herbarium, CALM. COMO. WA.
 Western Australian Laboratories, CSIRO. WEMBLEY. WA.
 Western Australian Naturalists Club. NEDLANDS. WA.
 Western Australian Wildlife Research Centre, CALM. WANNEROO. WA.
 Zeitschriftenstelle, MARBURG-LAHN. GERMANY.
 Zoological Society of Czechoslovakia. PRAHA. CZECHOSLOVAKIA.
 Zoologisches Institute. HAMBURG. GERMANY.

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